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by

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Re-examination of Geographical Cranial Variation in the Pantropical Spotted Dolphin *(Stenella attenuata)* in the Eastern Pacific

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Abstract.—The spotted dolphin (*Stenella attenuata*) is found throughout much of the eastern tropical Pacific Ocean. A previous study evaluated morphological variation in skull morphology, but now specimens are available for a greater portion of the range. Also, corrections have been made in data and an assessment made of repeatability of character measurements. We reassessed geographic variation in 30 cranial features (26 morphometric measures and 4 tooth counts) based on 611 museum specimens. All characters except two tooth counts showed statistically significant geographic variation, while 21 of the 30 characters exhibited significant sexual dimorphism. Males were larger in most characters; females are larger in some length measurements involving the rostrum and ramus. As in previous analyses, inshore *S. attenuata* were found to be very distinctive, so subsequent analyses focused on offshore spotted dolphins from 29 5° latitude-longitude blocks. Mantel tests and matrix correlations for 19 of the 30 features demonstrated significant "regional patterning," while 22 of the characters were shown to have "local patterning." Principal components, canonical variates, and cluster (UPGMA and function-point) analyses also were employed to assess geographic variation. In the eastern portion of the range, the subdivision between northern and southern offshore *S. attenuata* found in the previous investigation was confirmed. In general, blocks to the west (including one encompassing part of the Hawaiian Islands) were more like the southern blocks than blocks of the northeast. A general concentric pattern of geographic variation—similar to that found for the spinner dolphin (*S. longirostris*)—is suggested. Product-moment correlations, Mantel tests, and matrix correlations were used to assess covariation of morphological features and 13 environmental variables. Morphological patterns were similar to those found in a number of environmental variables, particularly water depth, solar insolation (January), sea surface temperature (January and July), surface salinity, and thermocline depth (winter and summer). Comparisons of morphological variation in spotted dolphins and spinner dolphins based on corresponding data for 16 blocks indicated strong correspondence in general trends summarized in the first principal components and first canonical variables. For the two species, geographic patterns in 13 of the 30 morphological characters showed statistical correspondence based on Mantel tests, while product-moment correlations were significant for 15 of the characters. These correlations based on data for corresponding blocks were positive for 12 characters, but negative for the length of the temporal fossa and the number of teeth in the upper left and upper right toothrows. Positive covariation probably reflects common natural selective factors, while the reverse trends for certain characters may be the result of competitive interspecific interactions. Present management units are inconsistent with the pattern of cranial variation;

spotted dolphins from west of 120°W probably should not be pooled with those to the east, as they show closer affinity with the Southern Offshore unit. In addition, the boundary between the Northern and Southern units should probably be moved north to about 5°N.

Spinner and spotted dolphins (*Stenella longirostris* and *S. attenuata*) have broadly overlapping ranges in the eastern tropical Pacific Ocean (Perrin et al. 1983). Information concerning geographic variation of these species is of both intrinsic scientific and practical interest. Dolphins in the region are killed as a result of purse-seining for yellowfin tuna (*Thunnus albacares*; Allen 1985). The tuna often are found in association with these two dolphin species (or with *Delphinus delphis*), and fisherman set nets on the dolphin schools to capture tuna found below the dolphins. Estimates indicated that in recent years roughly 53,000 to 129,000 dolphins have been killed annually as a result of fishing operations (Hall and Boyer 1987, 1988, 1989, 1990, 1991a, 1991b). Government regulations in the United States set limitations on U.S. vessels with respect to the extent of dolphin mortality that will be permitted. Dolphins are managed by defining a series of management stocks. Data, such as those on skull morphology, can provide insight as to underlying population subdivision and may be of considerable value in defining geographic boundaries of biologically relevant management stocks (Dizon et al. 1992).

Douglas et al. (1992) have provided a detailed assessment of geographic variation in cranial morphology of spinner dolphins. For spotted dolphins, the most recent geographic variation analyses using skull characteristics were by Douglas et al. (1984) and Schnell et al. (1986). Numerous additional specimens have become available, particularly from the western portion of the range and Hawaii. In addition, as indicated by Douglas et al. (1992) for spinner dolphins, an appraisal has been performed to determine the repeatability of 36 skull measures used in previous studies (Douglas et al. 1984; Schnell et al. 1986). Also, some specimens that were not fully adult had inadvertently been incorporated into the previous spotted dolphin analyses. For these reasons, we have undertaken a reassessment of geographic variation and sexual dimorphism of spotted dolphins from the eastern tropical Pacific. This provides an opportunity to reevaluate variation patterns previously described and to compare directly patterns of variation found in spotted and spinner dolphins.

Materials and methods

Overall, data-gathering and assessment procedures outlined by Douglas et al. (1992) were used. We measured 611 adult museum specimens (maturity evaluated on basis of premaxilla fusion with maxilla at distal end of rostrum; Dailey and Perrin 1973) of spotted dolphins (Fig. 1). These included 534 of 613 specimens used in an earlier studies (Douglas et al. 1984; Schnell et al. 1986; 79 specimens previously used had been incorrectly aged or had inadequate locality data) along with 77 new specimens.

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As was done with spinner dolphins (Douglas et al. 1992), the first specimen set was measured by M. E. Douglas and the new specimens by W. F. Perrin. In addition, Perrin remeasured 81 specimens of spinner and spotted dolphins measured by Douglas to determine whether measurements were repeatable. Initially, 36 characters were evaluated (illustrations and character definitions given in Schnell et al. 1985). Comparisons of measurements taken on the same specimens by the two investigators indicated that 6 of the original 36 measurements (i.e., W. Lf. Premax.[at midline of Nares], W. Rt. Premax.[at midline of Nares], Separation of Pterygoids, L. Lf. Tympanic Cavity, L. Rt. Tympanic Cavity, and W. at Pterygobasioocipital Sutures; abbreviations used in these and other character names are listed in footnote *a* of Table 1) should be deleted, because we were not able consistently to repeat these measurements. For some other measurements, there were differences between investigators, but the differences were consistent (e.g., one obtained measurements that were smaller than those reported by the other). Therefore, we calculated regression equations for each of the remaining characters based on the 81 jointly-measured specimens. These regression equations were used to convert the measurements from the rest of the initial specimens to appropriate values for inclusion with the measurements taken by Perrin. Through these procedures, we developed a data set of 30 characters (see Table 1) for the 611 specimens.

Specimens were not used if, because of damaged parts, we could not obtain most of the 30 measurements. Missing values (0.50% of total) for included specimens were estimated by linear regression ("Missing Data Estimator" program by Dennis M. Power, pers. comm.) onto the character that explained the greatest proportion of the variance for the variable being considered.

Animals were assigned to 5° latitude-longitude blocks, with each geographic block assigned a numerical code (see Fig. 1). These codes were modified slightly from those employed by Schnell et al. (1986) to accommodate new specimens from more westerly blocks. We had specimens available from 41 blocks, 8 of which were represented by only a single specimen and 4 of which were inshore blocks (i.e., contained only specimens of the inshore form; Douglas et al. 1984). The 29 blocks that were not inshore blocks and had more than one specimen were used as the basis for most geographic variation analyses. While several of the 29 blocks have relatively small samples, geographic-patterning tests (described below) suggested that, in general, sample values are representative of what is expected for these blocks based on their geographic positions.

Schnell et al. (1985) showed *S. attenuata* to be sexually dimorphic for 23 of 36 characters. Because some specimens used in that analysis were removed and new specimens added (see above), we conducted a two-way analysis of variance (ANOVA) for block and sex based on specimens in the 11 blocks with at least four of each sex (Fig. 1). Correction terms were obtained to adjust measurements of the larger sex downward and the smaller sex upward, thus producing sex-adjusted or "zwitter" measurements (method described in more detail by Schnell et al. 1985). As a result, we were able to combine specimens for both sexes in an overall analysis of geographic variation.

Correlation, ordination and clustering

After conversion to zwitters, characters were standardized (means = 0, standard deviations = 1). Product-moment correlations were computed among characters, and associations among characters were summarized by clustering characters (unweighted pair-group method with arithmetic averages; UPGMA). This technique is a type of hierarchical cluster analysis that also was used to summarize average distance coefficients (Sneath and Sokal 1973) calculated for all pairs of blocks based on standardized data. Cophenetic correlation coefficients indicate the extent to which distances in resulting dendrograms accurately represented original interblock morphologic distances.

Standardized data also were summarized using a nonhierarchical *K*-group method (function-point cluster analysis; described in Katz and Rohlf [1973] and Rohlf et al. [1979]). Using this technique, blocks are assigned to subgroups at a specified level. A *w*-parameter value used in function-point clustering was varied. A hierarchical but not necessarily non-overlapping system of clusters was obtained by repeating the analysis at different clustering levels. Results are displayed in modified skyline diagrams (Wirth et al. 1966).

Using standardized data, we constructed scatter diagrams by projecting blocks onto the first two principal components (Sneath and Sokal 1973) extracted from a matrix of correlations among the 30 characters. Canonical variates analysis also was employed to obtain the subset of variables that show the greatest interblock separation relative to intrablock variation (Program P7M of BMDP; Dixon 1990). Plots of the first two canonical variables show the maximum separation of blocks in two-dimensional space.

Mantel test for geographic patterning

A Mantel (1967) test was used to assess interlocality variation in each character and determine whether measures are geographically patterned or, alternatively, vary spatially at random. The observed association between sets of character differences and geographic distances was tested relative to its permutational variance, and the resulting statistic compared against a Student's *t*-distribution with infinite degrees of freedom. We performed analyses using GEOVAR, a computer-program library for geographic variation analysis (written by David M. Mallis and provided by Robert R. Sokal, State University of New York at Stony Brook).

Character differences were compared first with actual geographic distances (in nautical miles) between centers of blocks and then with reciprocals of distances. In evaluations of reciprocals, where distances are scaled in a nonlinear manner, longer distances are considered effectively to be equal, and the portion of the scale involving smaller distances is expanded. Thus, use of reciprocals of distances increases the power of analyses to reveal geographic patterns that are "local" in nature (i.e., involving closely placed blocks), whereas tests involving nautical-mile distances evaluate "regional" trends. Positive associations of character differences and nautical-mile distances are indicated by positive *t*-values, while negative *t*-values denote such associations

when using distance reciprocals. Douglas et al. (1992) provided a simplified example to demonstrate use of the Mantel procedure.

We also computed matrix correlations (Sneath and Sokal 1973) between character differences and the associated geographic distances or reciprocals of distances between localities. The statistical significance of these coefficients cannot be tested in the conventional way, because all pairs of localities were used and these are not statistically independent. However, the resulting values can be used as descriptive statistics indicating the degree of association of difference values.

Morphological-environmental covariation

We calculated product-moment correlations of block means for morphological characters with environmental variables. Data were available for 13 environmental variables for the eastern tropical Pacific Ocean (Table 2; data sources summarized in Douglas et al. 1992). The list of environmental variables used is somewhat different than that employed by Schnell et al. (1986), because data for some of the variables were not available for all blocks in the broader geographic range being considered in the current study. We also used UPGMA to summarize associations among these environmental variables for 51 blocks; since these two dolphin species have broadly overlapping distributions in the eastern tropical Pacific, the blocks used are representative of areas inhabited by *S. attenuata.*

In order to obtain summary variables reflecting overall environmental trends, we conducted a principal components analysis of the 13 environmental variables for 51 blocks with specimens of *S. longirostris* (Douglas et al. 1992) or *S. attenuata* or both. Individual blocks were projected onto the resulting environmental principal components based on standardized data. These environmental components served as composite environmental variables for comparisons with morphological variables.

Matrix correlations and Mantel tests were used to test for local and regional patterning of environmental variables. Also, differences between each pair of blocks for a given morphological variable were compared with those for an environmental variable.

Interspecific comparisons

The predominant trends in the data sets for each of *S. attenuata* and *S. longirostris* were summarized with principal components and canonical variables. Information is available for 16 blocks from which both offshore *S. attenuata* and *S. longirostris* were sampled (Fig. 1). These blocks are representative of the total geographic range investigated in our studies. In order to compare general patterns of variation in the two species, we calculated product-moment correlations, Mantel tests, and matrix correlations for individual morphological characters, principal component projections, and canonical variable projections of these 16 blocks.

In our analyses, average distances based on morphological characters were computed between each pair of localities. To evaluate the extent of similarity in geographic patterns, the original distance matrices for each species were modified such that only distances among the 16 localities common to both species were included. These matrices were then compared using the Mantel test and computing the matrix correlation.

Results

Sexual dimorphism

Table 1 includes mean measurements for males and females based on 11 blocks. For two-way ANOVAs assessing geographic block and sex (df = 21, 461), all but 5 of the 30 were very highly significant ($P < 0.001$). The probability was 0.02 for No. Teeth(Low.Rt.) and 0.007 for Orbital L. Two characters showed no significant variation (upper tooth counts) and one character (No. Teeth[Low.Lf.]) was close to significant ($P < 0.06$).

Statistically significant interactions ($P < 0.05$) between block and sex were found for five of the characters: Condylobasal L.; W. Rostrum(at 1/4 L.); W. Rostrum(at 1/2 L.); W. Rostrum(at 3/4 L.); and W. Internal Nares. Interaction denotes that the degree of sexual dimorphism differs among blocks for these characters.

Sexual dimorphism was significant for 22 of the 30 characters (Table 1). Females had a longer rostrum, which is reflected in a number of characters (i.e., 2, 3, 22, 27, 30). In general, males had wider skulls and tended to be larger for nonrostral portions of the skull. Percentage differences between sexes are presented in Table 1. The average absolute difference (i.e., sign ignored) between the sexes for the 30 characters was 1.78%. For 8 characters where females were larger, the average difference was 0.75%, while for 22 characters where males were larger the average difference was 2.16%. The greatest differences were found for W. Premax.(at 1/2 L.) and W. Rostrum(at 3/4 L.)—5.25% and 6.66%, respectively.

Correlation, ordination and clustering

Most character pairs had positive correlations. An exception was tooth counts and temporal fossa measurements, which tended to have negative correlations with skull width measurements. The dendrogram in Figure 2 summarizes absolute correlations (i.e., sign of correlation ignored) among characters based on 29 blocks to provide an assessment of character covariation. The W. External Nares was the character with the least association with other measures. Tooth characters join and are separated from the remaining morphometric characters. Braincase measures and Skull W.(at Parietals) cluster in another relatively distinct group. The remaining characters are arranged in two groups. The one at the top of Figure 2 includes most length measurements and Ht. Ramus. Width measurements along with L. Antorbital P., Orbital L., and L. Temporal Fossa are included in the adjoining major cluster (Fig. 2).

Table 3 includes character loadings on the first two principal components based on data for 29 blocks. Component I explains 45.0% of the total variance for the 30 characters, while component II summarizes an

additional 16.8% (cumulative total of 61.8%). Projections of blocks onto the two components are depicted in Figure 3, and a map (Fig. 4) is included that renders geographically block projections onto the first component. Component I represents general size, with relatively high character loadings (Table 3) for most characters, the exceptions being tooth characters and the two temporal fossa measurements. The specimens from blocks in the northeastern portion of the range tend to be small (Figs. 3 and 4), while those to the south and southwest typically are larger. The largest specimens are found in block 0802, which encompasses a portion of the Hawaiian Islands. Component II reflects tooth counts and measurement associated with toothrow length (Table 3). Blocks with relatively high values for these characters are found near the top of Figure 3, while those with low values tend to be near the bottom.

Blocks with single specimens were not used in the delineation of the principal components, but have been projected onto components calculated using the 29 blocks (Fig. 3). In general, the single-specimen blocks fall close to where one would predict based on their geographic position; some exceptions are expected based simply on expected chance variation.

Interblock morphological differences are summarized in the phenogram in Figure 5. Two blocks (0312 and 0802) are loosely joined in the most disparate cluster. Remaining blocks are divided into two clusters. The one represented at the top of Figure 3 includes the blocks from the south, southwest and west, while the other includes blocks from the northeastern portion of the range.

Clusters based on the function-point procedure are summarized in the modified skyline diagram in Figure 6A. The most distinctive block is 0802 (encompassing part of Hawaiian Islands) at the right of the diagram. A number of single blocks (0312, 0314, 0311) are separated from the others at *w*-values of 3.10 and 2.87. Most of the blocks from the northeastern portion of the range were included in a single cluster at lower *w*-values, although some individual blocks were separated by themselves (e.g., 0614, 0711).

In Figure 6B, a skyline diagram is included that is based on five characters: L. Rostrum(frm.Pterygoid); Preorbital W.; L. Braincase; L. Temporal Fossa; and W. Temporal Fossa. These variables were identified using canonical variates analysis (reported below) as those that in combination provided the greatest discrimination among blocks. Using function-point clustering on these selected characters provided clusters that persisted through several clustering levels. At the *w*-value of 1.38, four clusters were formed. The Hawaiian Island block (0802) is in a group by itself (on left side of Fig. 6B). The blocks to the south, southwest and west are in a second assemblage, while the northeastern blocks form the other major cluster. Block 0711 is separated in its own group. At *w*-values above 1.38, the second cluster is subdivided, with the southern blocks being included with some from the southwest.

Canonical variates analysis selected five characters (Table 4). Blocks are projected onto the first two canonical variables resulting from this analysis (Fig. 7), while Figure 8B shows geographically the distribution of projections onto canonical variable 1. The eigenvalue for canonical variable 1 is 1.00, while that for variable 2 is

0.19. The two together summarize 82.4% of the variance in the five characters. In the scatter diagram (Fig. 7), blocks with only single specimens are projected onto the canonical variables generated using the other 29 blocks. As indicated in Table 4, the most important character in the canonical variates analysis was Postorbital W. (Fig. 8A). It has relatively small values in the northeastern portion of the range, and considerably larger values in other areas to the south, southwest and west. The largest Postorbital W. measurements are found in specimens taken near the Hawaiian Islands (0802). The geographic configuration of this character is very similar to the general pattern exhibited by the first canonical variable (Fig. 8B). Canonical variable 1 and principal component I (Fig. 4) have similar geographic patterns. Canonical variable 2 does not reflect any particular geographic pattern. It basically contrasts three blocks (0711, 0802, and 0311) with the others, as indicated by these three being separated in the upper portion of Figure 7 from other blocks.

Mantel test for geographic patterning

Results of Mantel tests and matrix correlations comparing interblock character differences with geographic distances (in nautical miles) and with the reciprocals of geographic distances are presented in Table 5. Regional patterning, as indicated by a significant association with geographic distance, was found for 18 (60.0%) of the 30 characters. In these characters, the localities the furthest apart tended to exhibit the greatest morphological difference. Local patterning, which is judged based on a significant negative association between geographic distance reciprocals and morphological differences, was found in 22 (73.3%) of the characters. Not unexpectedly, virtually all characters (i.e., all but one) exhibiting significant regional pattern also showed local patterning.

Our tests showed strong regional and local patterning for principal component I and canonical variable 1, while principal component II has significant local patterning (Table 5). Mantel tests and correlations confirm a point made earlier—that canonical variable 2 does not exhibit a systematic geographic pattern.

Morphological-environmental covariation

Douglas et al. (1992: fig. 9) included a dendrogram summarizing absolute correlations among 13 environmental variables (listed in Table 2) for blocks having either *S. attenuata* or *S. longirostris* or both. These variables were partitioned into five clusters. Sea Current(N., Winter) is separated by itself, while Sea Current(W., Winter) and Oxygen Min. Layer(Depth) form a second cluster, which groups with an assemblage of five variables involving surface measures of temperature, oxygen, and salinity (variables 6, 7, 8, 10 and 13). The fourth cluster has the two solar insolation variables (4 and 5), while the fifth includes three measures indicating water and thermocline depths (variables 3, 11, and 12).

A principal components analysis was conducted to obtain variables that would summarize general environmental trends, with three components being presented in Douglas et al. (1992: table 6). Highest

loadings for environmental variables on principal component I included those for sea surface temperatures (variables 6, 7, and 8), particularly July temperatures. The correlation with Sea Surface Temp.(Ann.Var.) is negative. The second component reflected thermocline depth (variable 11 and 12), as well as Water Depth and Surface Salinity. The third had relatively high loadings with the two characters involving solar insolation (variables 4 and 5). A more detailed description of character associations with the principal components is available in Douglas et al. (1992).

Projection values for environmental principal component I are summarized in Figure 9A for the 29 blocks with larger samples of *S. attenuata*. It reflects the fact that sea surface temperatures are considerably higher in northern than southern blocks, and that the northern blocks exhibit relatively little annual variation in surface temperatures. Block projections on environmental principal component II are portrayed in Figure 9B, which summarizes the increases in thermocline depth, Water Depth, and Surface Salinity as one proceeds west and south.

Correlations of morphologic variables, principal components, and canonical variables with environmental variables and environmental principal components are summarized in Table 6. The sea current measures (variables 1 and 2) have virtually no statistical association with morphological characters, while Water Depth (variable 3) has positive correlations with lengths and widths of the rostrum, as well as principal component I and canonical variable 1 (Table 6).

Solar Insolation (Jan.), the fourth variable, has larger values in the north, with values becoming smaller to the south. It has significant positive correlations with nine morphologic variables, and negative associations with six others. The negative associations with the two temporal fossa measures are particularly strong (W. Temporal Fossa summarized in Fig. 10A). This environmental variable has relatively high correlations with canonical variable 1 and principal component II (Table 6).

Not unexpectedly, the fifth variable, Solar Insolation(Annual) exhibits high values at the equator. Readings are lower for blocks closer to either pole. It has few significant statistical associations with morphologic characters, although the negative correlations with L. Braincase and W. Temporal Fossa (Fig. 10A) are relatively high (Table 6).

The sixth and seventh environmental measures (surface temperatures in January and July) have negative associations with a number of width measurements, as well as with a few length variables (Table 6). They have very strong positive correlations with temporal fossa measures. Figure 10 summarizes the values for Sea Surface Temp.(July), as well as for the closely associated W. Temporal Fossa (r = 0.799; the highest correlation of an environmental and a morphological variable). Sea Surface Temp.(Ann. Var.), the eighth environmental variable, has significant correlations with relatively few morphologic characters (Table 6), although its pattern has affinities with those summarized by principal component II and canonical variable 1. Environmental

variable 9, Oxygen Min. Layer (Depth), shows very few statistically significant correlations with morphological measurements (Table 6).

Surface Salinity, variable 10, exhibits strong covariation with numerous measurements, particularly those involving the anterior portion of the skull (Table 6). It also has high correlations with principal component I (Fig. 4) and canonical variable 1 (Fig. 8B). Salinity, which was depicted in Douglas et al. (1992: fig. 13B) for *S. longirostris* blocks, shows east-west changes from lower to higher values at a given latitude, as well as a north-to-south trend of increasing values (below 15° N).

The eleventh variable, Thermocline Depth (Winter), is summarized in Figure 11B. It has positive correlations with 12 morphological measures and a negative correlation with 1 character. The correlation of this environmental variable with Skull W.(at Parietals), shown in Figure 11A, is 0.610. Variable 12, Thermocline Depth (Summer), has strong positive correlations with a large number of variables, particularly those reflecting measurements in the anterior portion of the skull. Given its covariation with Water Depth, it is not surprising that Thermocline Depth (Winter) has significant correlations with principal component I and canonical variable 1. Surface Dissolved Oxygen (variable 13) has only a few weak statistical associations with morphological characters.

Environmental principal component I (Fig. 9A) has a pattern similar to those for sea surface temperatures in January and July (variables 6 and 7). The highest correlation (0.733) of this component is with W. Temporal Fossa (Fig. 10A). The second environmental component (Fig. 9B) is strongly associated with numerous characters (Table 6), reflecting the general trends from the northeast to the west, southwest, and south. The third component, which is negatively associated with canonical variable 2 (Table 6), has only one strong association with a morphological variable, that being with Tooth W. (r = -0.680; Table 6). The third environmental component exhibits decreasing values as one moves away from the equator. Tooth W. shows an opposite pattern, which is particularly emphasized with the relatively wide teeth in specimens from the Hawaiian Islands (block 0802).

In Table 7, Mantel t-values and matrix correlations are provided for associations of environmental variables (including environmental principal components) with the five morphologic characters selected for inclusion during the canonical variates analysis. With this approach, covariation patterns are assessed on the basis of difference values between all block pairs. Preorbital W. shows a strong association with Water Depth, the two measures of solar insolation, the sea surface temperatures in January and July, Oxygen Minimum Layer(Depth), and Surface Salinity (Table 7). It also exhibits a pattern that is statistically associated with all three environmental components. The two measures of the temporal fossa show concordance with patterns for solar insolation (January, as well as annual), all sea surface temperature measures, Oxygen Minimum Layer(Depth), Surface Salinity, and the first environmental principal component. The L. Temporal Fossa also has a weak statistical association with environmental component III. Table 7 indicates that the pattern for

L. Rostrum(frm.Pterygoid) is associated statistically with those for Water Depth and Thermocline Depth(Summer). This morphologic character also is shown to have geographic patterning statistically similar to that exhibited by environmental components II and III. For L. Braincase, the Mantel tests were significant (but weak) only for Sea Current(N., Winter) and Solar Insolation(Jan.). The strongest association of L. Braincase is with environmental component III; its pattern also is linked statistically to the second environmental component.

Interspecific comparisons

The study by Douglas et al. (1992) reported comparable statistical analyses on skulls of *S. longirostris,* a dolphin species that overlaps broadly with *S. attenuata* in the eastern tropical Pacific. The projections onto the first two principal components for *S. attenuata* were evaluated against projections on the two components obtained for *S. longirostis* (for summary information on these components, see Fig. 3 and Table 3 for offshore *S. attenuata*, and fig. 3 and table 3 of Douglas et al. [1992] for *S. longirostris*). A strong correspondence exists between the first principal components for the two species, as indicated by product-moment correlations, Mantel *t*-tests, and matrix correlations comparing the component projections. The second principal components for the two studies are not similar (Table 8); they summarize different general trends in variation.

A similar interspecific comparison was made of projections of the 16 blocks onto canonical variables (Table 9). The first canonical variable for *S. attenuata* and that for *S. longirostris* are virtually identical, reflecting highly concordant geographic patterns for the two species (Table 8). While block projections on the first canonical variables for the two species were very similar, the actual characters incorporated into the canonical variables are not the same (see our Table 4 and table 4 of Douglas et al. 1992). Of the five characters entered for each species, only L. Rostrum(frm.Pterygoid) was present in both character sets. However, the first and most important character entered into the analyses—Preorbital W. for *S. attenuata* and Postorbital W. for *S. longirostris* are highly correlated (see close association of these two characters in *S. attenuata* indicated in Fig. 2); because these two characters exhibit very similar variation patterns, a canonical variates analysis typically would not select both for inclusion, since they provide basically the same information for separating blocks.

The second canonical variables for the two studies also were compared (Table 8). They showed no statistical association.

Table 10 includes results of Mantel tests, matrix correlations, and product-moment correlations of interspecific comparisons for individual morphological characters. Thirteen of the 30 *t*-values for Mantel tests of interlocality differences for the same character in the two species were significant, while 15 of 30 product-moment correlations indicated statistical associations. Nine of 11 characters with positive correlations were width measures. Furthermore, a tenth (L. Antorbital P.) is essentially a width character as well (for illustration of measurement, see Schnell et al. 1985). The two characters involving upper tooth counts, as well

as L. Temporal Fossa, exhibited significant negative correlations. For *S. attenuata*, upper tooth counts tend to be higher for the western blocks (but not for the Hawaiian Island block), while in *S. longirostris*, higher upper tooth counts are found in the Hawaiian and eastern blocks. The L. Temporal Fossa is greater in northern localities of *S. attenuata* (Fig. 10A), while the shorter fossae are found in northeastern blocks for *S. longirostris* (see Douglas et al. 1992: fig. 11).

Discussion

Sexual dimorphism

Schnell et al. (1985) conducted the most recent analysis of sexual dimorphism of *S. attenuata* in cranial morphology. They found statistically significant dimorphism for 23 of 36 characters. Our analyses used many of the same specimens, with some added and some deleted, and 30 of the same characters. For the 30 characters we analyzed, they found the same 22 to have statistical differences between sexes. Results from the two studies on sexual dimorphism are essentially the same. Thus, for *S. attenuata*, our current findings simply update information in Schnell et al. (1985) to reflect a modified sample sizes and a reduced character set.

Douglas et al. (1992) analyzed sexual dimorphism in skull measures for *S. longirostris* from the eastern tropical Pacific. They found 15 of the 30 characters to be statistically different between sexes. Since *S. longirostris* samples are somewhat smaller, one might expect fewer significant differences in this species simply due to sample size. Nevertheless, inspection of the results indicates support for the conclusion reached by Douglas et al. (1986: 542-543) "that the degree of sexual dimorphism in spotted dolphins is greater than in spinner dolphins." They also pointed out that "the trends are basically the same for both species, suggesting that common behavioral and/or ecological factors are influencing sexual dimorphism in these dolphins."

Geographic variation

From an initial group of specimens, Perrin et al. (1979b) described differences between dolphin skulls available from southern areas and those from more northerly locations. Schnell et al. (1986), based on larger sample sizes, indicated that available information "strongly implies a significant degree of isolation between northern and southern forms." They did not have specimens from west of 125°W and called for additional material from west of 120°W to help clarify the relationship between southern *S. attenuata* and other populations, particularly in light of the notation by Perrin et al. (1979b) of similarities of specimens from the southern group with those from Hawaii.

In the eastern portion of the range, the subdivision between northern and southern offshore *S. attenuata* found previously by Perrin et al. (1979b) and Schnell et al. (1986) was confirmed by our analyses with an geographically expanded specimen base. In general, blocks to the west (including those from the waters adjacent to Hawaii) are more like the southern blocks than blocks of the northeast. We found a general

concentric pattern of geographic variation (see Fig. 8B), much like that established by Douglas et al. (1992) for the broadly overlapping *S. longirostris*.

Reilly (1990) provided some insight at to possible reasons why samples of *S. attenuata* and *S. longirostris* from the south, southwest, and west would show close morphologic affinities. He analyzed large-scale dolphin distribution patterns and environmental patterns based on research-vessel surveys conducted in the eastern tropical Pacific from June through November, comparing his results with those of Au and Perryman (1985). Reilly's (1990) distributional comparisons between seasons indicated that along 10°N *S. attenuata* and *S. longirostris* occur in relatively high density west of 120°N during the summer. Furthermore, they were not in high densities along 4°N between 90 and 120°W, and along 6°N between 88 and 110°W—regions with relatively high concentrations of these two species in the winter (Au and Perryman 1985). Reilly (1990) indicated that "One hypothesis suggested by these complementary changes is an intraregional, seasonal movement." Data from mark-recapture efforts (Perrin et al. 1979a, Hedgepeth 1985) are consistent with respect to the hypothesized direction of such migrations, although the distances are greater than those suggested by the very limited data from these studies. Reilly (1990) also noted that the suggested movement patterns are at least partially explainable based on seasonal atmospheric and oceanographic changes in the region.

Morphological-environmental covariation

In the earlier study of *S. attenuata,* Schnell et al. (1986) assessed environmental-morphological covariation for a similar, although not identical, set of environmental parameters. Since their investigation was restricted largely to eastern blocks, different findings with respect to covariation are possible. Schnell et al. (1986) noted that the strongest morphological-environmental associations involved Solar Insolation(Jan.). Sea surface temperatures also covaried with a number of morphological characteristics, as did Oxygen Min. Layer(Depth).

The environmental principal components indicated that a number of environmental measures have a north-south component (see Fig. 9A), while others (particularly thermocline depth and water depth) show trends from the east to the west, southwest, and south. Not unexpectedly, a mosaic of variation patterns are present in the suite of morphologic characters we assessed. Some, like W. Temporal Fossa (Fig. 10A), align closely with environmental variables—such as Sea Surface Temp.(July) (Fig. 10B)—subsumed under environmental component I (Fig. 9A). Others, like Skull W.(at Parietals)(Fig. 11A), display patterns similar to those of Thermocline Depth(Winter) (Fig. 11B) and other environmental measures summarized by environmental component II (Fig. 10B) However, the overall, general morphological trend is reflected best by projections onto the first canonical variable based on morphologic data (Fig. 4), which has a relatively strong negative correlation with environmental component I and a weaker positive one with environmental component II.

By adding the more westerly blocks to the analysis, environmental-morphological covariation patterns that emerged, in some cases, were different from those reported by Schnell et al. (1986). For example, statistically significant correlations of several morphologic characters with Sea Current (N., Winter) and Sea Surface Temp.(Ann. Var.) were mostly eliminated. Likewise, strong associations with measures of solar insolation were substantially reduced for all but a few characters (i.e., L. Braincase, L. Temporal Fossa, and W. Temporal Fossa; Table 6). Some characters, such as Sea Current(W. Winter) and Oxygen Min. Layer(Depth), did not have variation patterns in either study that corresponded to those for morphologic variables. Water Depth, however, has significant correlations with more characters now that western blocks have been added. At least three environmental measures—Sea Surface Temp.(Jan.), Sea Surface Temp.(July)(Fig. 10B), and Surface Salinity—had relatively strong covariation patterns that stayed relatively constant through the two studies.

Interspecific covariation

In this paper we have presented statistical data for trends in geographic covariation of *S. longirostris* and *S. attenuata* skulls from 16 blocks for which samples of both species were available (brief comments on covariation were included by Douglas et al. 1992). Geographic patterns in 13 of the 30 morphological characters showed statistical correspondence based on Mantel tests, while product-moment correlations were significant for 15 characters. Some of these associations were very strong (i.e., correlations as high as 0.883; see Table 9). Given that we are comparing two species, entities that have independent gene pools, the most likely explanation for common positive trends in morphologic covariation is that the two species are being subjected to similar forces of natural selection.

However, we found several striking examples where covariation was negative. A significant negative association was found for L. Temporal Fossa, while the negative correlation for W. Temporal Fossa was nearly significant statistically. The number of upper teeth (characters 23 and 24) also show significant negative correlations (Table 9). Muscles associated with the feeding apparatus are positioned in the temporal fossa; obviously, tooth numbers could be related to prey types taken. One suspects that the presence of antithetical trends in these particular skull characteristics is a result of competitive interactions involving these two interacting species. This may be an example of ecological character displacement related to differences in feeding and food types taken (Perrin 1984). Certainly, the two species are found in close association over much of the eastern tropical Pacific (Au and Perryman 1985, Reilly 1990); 49% of *S. attenuata* schools included some *S. longirostris,* while 73% of the schools of the less common *S. longirostris* included *S. attenuata* (Reilly 1990).

Genetic subdivision, management units and implications of cranial variation

The results suggest that gene flow is not uniform throughout the range of *S. attenuata* in the eastern Pacific; the morphological heterogeneity probably reflects genetic subdivision, a conclusion also reached as a result of the

earlier study by Schnell et al. (1986). A similar inference was drawn by Douglas et al. (1992) based on morphologic studies of *S. longirostris*. For *S. attenuata*, we found that 93.3% of the 30 morphologic characters had statistically significant geographic variation, with 60.0% exhibited regional patterning and 73.3% local patterning. This geographic partitioning of morphologic variance was demonstrable even with pooling of specimens taken over a number of months and years, a process that would tend to shroud such relationships.

The boundaries of the stock units presently employed in management (Perrin et al. 1985) are not fully consistent with the general pattern of morphologic variation described here. It appears that animals west of about 120°W longitude have greater affinity with those in the Southern Offshore management unit than they do with *S. attenuata* from the eastern portion of the present Northern Offshore unit, the unit in which they are presently included. Further, the present boundary between the Northern and Southern Offshore units, at 1°S latitude, is probably too far south; a boundary at about 5°N would be more consistent with the general pattern of cranial variation.

The Northern Offshore unit bounded by 5°N and 120°W would be nearly congruent with the "conservation zone" suggested for *S. longirostris* (Perrin et al. 1991). This is to be expected based on the correlated trends of covariation with environmental variables; the two species, as they exist in this region, apparently are parts of an endemic fauna uniquely adapted to the far eastern tropical Pacific and, as such, are "evolutionarily significant units" (ESUs; Dizon et al. 1992).

The cranial results are only one line of evidence useful for delineation of management units; others, such as patterns in movements, external morphology or life-history parameters, also should be taken into consideration. For example, other data may indicate that *S. attenuata* west of 120°W differ significantly in some regard from those south of 5°N and should be managed separately (yielding three management units instead of the present two). Certainly, the specimens from the Hawaiian Islands are generally larger than those from the south, southwest, and west with which they have their closest morphologic affinity.

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Table 1

Geographic variation and sexual dimorphism in *Stenella attenuata* evaluated for 30 characters.

	Character[a]	*F*-value[b]		Mean[c]		Correction	Percentage
		Block	Sex	Male	Female	factor[d]	difference[e]
1	Condylobasal L.	10.59***	1.94	397.0	398.2	-0.74	-0.30
2	L. Rostrum(frm.Base)	6.94***	13.49***	236.7	239.5	-1.55	-1.20
3	L. Rostrum(frm.Pterygoid)	6.88***	6.84**	278.5	281.0	-1.31	-0.87
4	W. Rostrum(at Base)	14.20***	25.13***	83.3	81.8	0.73	1.85
5	W. Rostrum(at 1/4 L.)	12.25***	51.82***	57.1	55.2	0.90	3.32
6	W. Rostrum(at 1/2 L.)	13.82***	47.61***	42.4	40.9	0.78	3.78
7	W. Premax.(at 1/2 L.)	8.51***	72.88***	23.6	22.4	0.60	5.25
8	W. Rostrum(at 3/4 L.)	8.65***	73.90***	29.9	28.0	0.96	6.66
9	Preorbital W.	16.92***	45.92***	149.5	146.6	1.43	1.97
10	Postorbital W.	22.46***	42.23***	167.8	165.1	1.31	1.63
11	Skull W.(at Zygomatic P.)	21.98***	51.05***	167.4	164.5	1.46	1.79
12	Skull W.(at Parietals)	5.73***	54.11***	129.6	136.4	1.58	2.34
13	Ht. Braincase	10.61***	53.87***	95.9	93.7	1.04	2.36
14	L. Braincase	15.67***	39.94***	113.1	111.2	0.95	1.71
15	Max. W. Premax.	8.89***	4.45*	66.2	65.7	0.27	0.85
16	W. External Nares	7.38***	0.03	42.5	42.5	0.01	0.02
17	L. Temporal Fossa	22.41***	16.79***	70.1	68.4	0.82	2.53
18	W. Temporal Fossa	20.60***	28.50***	55.2	53.2	0.93	3.72
19	Orbital L.	2.97**	0.06	47.4	47.4	0.02	0.10
20	L. Antorbital P.	8.33***	4.30*	36.9	36.4	0.24	1.43
21	W. Internal Nares	9.58***	12.80***	47.4	46.6	0.36	1.58
22	L. Up. Toothrow	6.20***	10.56**	204.3	206.7	-1.29	-1.16
23	No. Teeth(Up.Lf.)	0.96	1.54	41.4	41.2	0.10	0.47
24	No. Teeth(Up.Rt.)	0.98	0.65	41.3	41.1	0.07	0.33
25	No. Teeth(Low.Lf.)	2.89*	0.02	41.0	40.9	-0.01	-0.02
26	No. Teeth(Low.Rt.)	2.82**	1.02	40.8	41.0	-0.08	-0.36
27	L. Low. Toothrow	5.38***	11.63***	198.6	201.2	-1.40	-1.28

Table 1 (continued)

Character[a]	*F*-value[b]		Mean[c]		Correction factor[d]	Percentage difference[e]
	Block	Sex	Male	Female		
28 Ht. Ramus	16.13***	0.12	57.3	57.1	0.38	0.24
29 Tooth W.	12.14***	19.65***	3.4	3.3	0.06	3.55
30 L. Ramus	9.02***	8.86**	335.5	338.3	-1.48	-0.82

[a]Abbreviations: frm. = from; Ht. = height; L. = length; Lf. = left; Low. = lower; Max. = maximum; No. = number; P. = process; Premax. = premaxillary; Rt. = right; Up. = upper; W. = width.

[b]*F*-values from main effects two-way analysis of variance (5^{O} block *vs.* sex) involving 11 blocks (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Total of 170 individuals. Degrees of freedom 10 for among-block variation and 1 for between sexes.

[c]Unweighted mean for 11 blocks.

[d]Added to all individual female measurements and subtracted from all individual male measurements to correct for sexual differences.

[e]Difference between sexes (males minus females) multiplied by 100, with the resulting value divided by average of male and female means.

Table 2

Environmental measurements compiled for each 5° latitude-longitude block.[a]

1	Sea Current (N., Winter)—Average northern component (in knots) of surface water current in winter.
2	Sea Current (W., Winter)—Average western component (in knots) of surface water current in winter.
3	Water Depth—Average sea depth (in m).
4	Solar Insolation (Jan.)—Average incoming solar radiation for January (in gm·cal/cm^2).
5	Solar Insolation (Annual)—Average annual incoming solar radiation in gm·cal/cm^2).
6	Sea Surface Temp. (Jan.)—Average January sea surface temperature (in °C).
7	Sea Surface Temp. (July)—Average July sea surface temperature (in °C).
8	Sea Surface Temp. (Ann. Var.)—Average annual sea surface temperature variation (in °C).
9	Oxygen Min. Layer (Depth)—Annual mean depth (in m) of absolute oxygen minimum surface with respect to the vertical.
10	Surface Salinity—Average salinity (°/oo) of surface sea water.
11	Thermocline Depth (Winter)—Mean depths (in m) to top of thermocline for January, February and March.
12	Thermocline Depth (Summer)—Mean depths (in m) to top of thermocline for July, August and September.
13	Surface Dissolved Oxygen—Annual mean dissolved oxygen (ml/l) of surface sea water.

[a]Data sources listed in Douglas et al. (1992: table 2). Abbreviations: Ann. Var. = Annual Variation; Jan. = January; Min. = Minimum; N. = North; Temp. = Temperature; W. = West.

Table 3

Principal component loadings for offshore *Stenella attenuata* involving character means for 29 blocks.

	Character	Component[a] I	Component[a] II
1	Condylobasal L.	**0.812**	-0.505
2	L. Rostrum(frm.Base)	0.786	-0.483
3	L. Rostrum(frm.Pterygoid)	0.795	-0.446
4	W. Rostrum(at Base)	**0.867**	0.206
5	W. Rostrum(at 1/4 L.)	**0.923**	0.157
6	W. Rostrum(at 1/2 L.)	**0.855**	0.308
7	W. Premax.(at 1/2 L.)	**0.863**	0.161
8	W. Rostrum(at 3/4 L.)	**0.868**	0.211
9	Preorbital W.	**0.930**	0.235
10	Postorbital W.	**0.940**	0.181
11	Skull W.(at Zygomatic P.)	**0.938**	0.173
12	Skull W.(at Parietals)	0.740	0.270
13	Ht. Braincase	-0.002	0.225
14	L. Braincase	0.508	-0.325
15	Max. W. Premax.	0.366	-0.059
16	W. External Nares	0.286	-0.311
17	L. Temporal Fossa	-0.544	-0.576
18	W. Temporal Fossa	-0.375	-0.541
19	Orbital L.	0.655	-0.018
20	L. Antorbital P.	**0.805**	0.203
21	W. Internal Nares	0.604	0.000
22	L. Up. Toothrow	0.705	-0.588
23	No. Teeth(Up.Lf.)	-0.137	**-0.668**
24	No. Teeth(Up.Rt.)	-0.112	**-0.726**
25	No. Teeth(Low.Lf.)	-0.301	**-0.673**
26	No. Teeth(Low.Rt.)	-0.341	**-0.635**
27	L. Low. Toothrow	0.680	**-0.632**

Table 3 (continued)

	Character	Component[a] I	Component[a] II
28	Ht. Ramus	0.608	0.355
29	Tooth W.	-0.129	0.118
30	L. Ramus	**0.803**	-0.528

[a]Relatively high loadings highlighted in bold as follows: (component I) > |0.8|; (II) > |0.6|.

Table 4

Canonical variates analysis of all specimens from 29 blocks.

	Character	*F*-value to enter	Order of entry	Coefficients[a] 1	Coefficients[a] 2
3	L. Rostrum(frm.Pterygoid)	2.88	4	0.0062 (0.0665)	-0.0731 (-0.7900)
9	Preorbital W.	9.19	1	0.1932 (0.8774)	0.0031 (0.3650)
14	L. Braincase	2.53	5	-0.0266 (-0.0851)	0.2243 (0.7179)
17	L. Temporal Fossa	2.84	3	-0.1113 (-0.4674)	0.0895 (0.3759)
18	W. Temporal Fossa	7.22	2	-0.1167 (-0.4305)	-0.0812 (-0.2996)
	Constant			-13.5670	-18.3837

[a]Unstandardized coefficients (with standardized values in parentheses) for canonical variates.

Table 5

Association of interlocality character differences with geographic distances (in nautical miles) and the reciprocals of these distances. Results from Mantel tests (*t*) and matrix correlations (*r*) for offshore *Stenella attenuata*.

	Distance		Reciprocal of distance	
Character	*t*	*r*	*t*	*r*
1 Condylobasal L.	4.19***	0.460	-4.19***	-0.303
2 L. Rostrum(frm.Base)	4.34***	0.449	-4.45***	-0.310
3 L. Rostrum(frm.Pterygoid)	3.59***	0.352	-4.10***	-0.276
4 W. Rostrum(at Base)	4.53***	0.493	-5.07***	-0.365
5 W. Rostrum(at 1/4 L.)	4.11***	0.446	-4.84***	-0.348
6 W. Rostrum(at 1/2 L.)	3.76***	0.413	-4.73***	-0.343
7 W. Premax.(at 1/2 L.)	1.28	0.134	-2.88**	-0.203
8 W. Rostrum(at 3/4 L.)	3.14**	0.347	-4.11***	-0.300
9 Preorbital W.	5.00***	0.464	-6.83***	-0.445
10 Postorbital W.	4.61***	0.397	-6.66***	-0.416
11 Skull W.(at Zygomatic P.)	4.22***	0.380	-6.21***	-0.398
12 Skull W.(at Parietals)	4.81***	0.583	-4.34*	-0.336
13 Ht. Braincase	1.81	0.227	-1.81	-0.143
14 L. Braincase	2.60**	0.339	-1.85	-0.151
15 Max. W. Premax.	1.64	0.159	-3.53***	-0.236
16 W. External Nares	0.78	0.066	-1.38	-0.085
17 L. Temporal Fossa	1.49	0.152	-3.13**	-0.216
18 W. Temporal Fossa	0.90	0.097	-2.86**	-0.206
19 Orbital L.	-0.25	-0.031	-0.35	-0.027
20 L. Antorbital P.	0.89	0.078	-3.65***	-0.229
21 W. Internal Nares	0.44	0.046	-1.09	-0.077
22 L. Up. Toothrow	4.08***	0.422	-3.93***	-0.274
23 No. Teeth(Up.Lf.)	1.57	0.173	-1.68	-0.123
24 No. Teeth(Up.Rt.)	3.03**	0.296	-3.68***	-0.247

Table 5 (continued)

	Distance		Reciprocal of distance	
Character	*t*	*r*	*t*	*r*
25 No. Teeth(Low.Lf.)	1.75	0.188	-1.89	-0.135
26 No. Teeth(Low.Rt.)	2.44*	0.283	-2.39*	-0.180
27 L. Low. Toothrow	2.99**	0.364	-3.20**	-0.249
28 Ht. Ramus	1.74	0.181	-1.69	-0.116
29 Tooth W.	3.36***	0.398	-3.82***	-0.292
30 L. Ramus	3.02**	0.361	-2.88**	-0.221
Component I	4.54***	0.474	-5.51***	-0.386
Component II	1.42	0.122	-2.75**	-0.172
Canonical Variable 1	3.76***	0.289	-6.69***	-0.393
Canonical Variable 2	1.11	0.143	-1.47	-0.119

Table 6

Product-moment correlations of block means for morphological variables and components versus environmental variables and components based on 29 blocks of offshore *Stenella attenuata*[a].

	Environmental variable[b]													Environmental component		
Character	1	2	3	4	5	6	7	8	9	10	11	12	13	I	II	III
1 Condylobasal L.			++							+	++	+++			+++	
2 L. Rostrum(frm.Base)			++								++	+++			+++	
3 L. Rostrum(frm.Pterygoid)			++							+	+	+++			++	
4 W. Rostrum(at Base)			++			–	-			+++	++	+++			+++	
5 W. Rostrum(at 1/4 L.)			++			—	–			+++	+	++		–	++	
6 W. Rostrum(at 1/2 L.)			+	+		—	—	+		+++		+		–	+	
7 W. Premax.(at 1/2 L.)			+	+		–	–			++		+		–		
8 W. Rostrum(at 3/4 L.)			++	+		–	–			+++		+		-	+	
9 Preorbital W.			+++	+		—	—			+++	+	++		–	++	
10 Postorbital W.			+++	+		—	—			+++		++		–	++	
11 Skull W.(at Zygomatic P.)			++			—	—	+	-	+++		++		—	+	
12 Skull W.(at Parietals)				-	-						+++				++	
13 Ht. Braincase											++					
14 L. Braincase				–	—						++					—
15 Max. W. Premax.				+		–	–			++		++		-		
16 W. External Nares	-															
17 L. Temporal Fossa				—	-	+++	+++	–		—		-	–	+++		
18 W. Temporal Fossa				—	—	+++	+++	—		—				+++		-
19 Orbital L.						-	-		-	++				–		

Table 6 (continued)

Character	Environmental variable[b]													Environmental component		
	1	2	3	4	5	6	7	8	9	10	11	12	13	I	II	III
20 L. Antorbital P.				++		—	—	+	–	+++		+		—		
21 W. Internal Nares						—	–	+	-	++				-		
22 L. Up. Toothrow		-	+					-			++	+++			+++	
23 No. Teeth(Up.Lf.)	++												-			
24 No. Teeth(Up.Rt.)													-			+
25 No. Teeth(Low.Lf.)			-			++				-				+		
26 No. Teeth(Low.Rt.)						+				-	-		-		-	
27 L. Low. Toothrow			+								+	++			++	
28 Ht. Ramus																
29 Tooth W.			-	-	–											—
30 L. Ramus			+								++	+++			++	
Component I			++			—	–			+++	+	+++		-	++	
Component II				++		–	–	+++		+			++	–		
Canonical Variable 1			+++	+++	+	—	—	++		+++		++		—	+	
Canonical Variable 2					-											—

[a]Blanks indicate nonsignificant correlations. Individual symbols refer to significant positive or negative correlations ($P<0.05$; greater than 0.367), double symbols indicate highly significant correlations ($P<0.01$; greater than 0.470), and triple symbols represent very highly significant correlations ($P<0.001$; greater than 0.580).

[b]Environmental variables: (1) Sea Current (N., Winter); (2) Sea Current (W., Winter); (3) Water Depth; (4) Solar Insolation (Jan.); (5) Solar Insolation (Annual); (6) Sea Surface Temp. (Jan.); (7) Sea Surface Temp. (July); (8) Sea Surface Temp. (Ann. Var.); (9) Oxygen Min. Layer (Depth); (10) Surface Salinity; (11) Thermocline Depth (Winter); (12) Thermocline Depth (Summer); and (13) Surface Dissolved Oxygen.

Table 7

Results of Mantel tests (*t*) and matrix correlations (*r*) for offshore *Stenella attenuata*. Comparison of interlocality differences for 13 environmental variables and 3 environmental components against those for five morphological variables selected in canonical variates analysis.

	Preorbital W.		W. Temporal Fossa		L. Temporal Fossa		L. Rostrum(frm.Pterygoid)		L. Braincase	
Environmental variable	*t*	*r*	*t*	*r*	*t*	*r*	*t*	*r*	*t*	*r*
1 Sea Current(N.,Winter)	-1.34	-0.114	2.43*	0.318	-0.20	-0.026	0.67	0.085	2.41*	0.322
2 Sea Current(W.,Winter)	0.02	0.001	-1.95	-0.139	-1.68	-0.119	1.94	0.136	0.82	0.059
3 Water Depth	4.12***	0.259	-0.45	-0.033	-1.08	-0.080	3.24**	0.236	1.17	0.088
4 Solar Insolation(Jan.)	7.38***	0.466	6.39***	0.479	6.47***	0.481	-0.56	-0.041	-2.29*	-0.173
5 Solar Insolation(Ann.)	7.58***	0.502	2.85**	0.238	2.91**	0.241	0.68	0.056	-0.84	-0.071
6 Sea Surface Temp.(Jan.)	5.53***	0.371	5.71***	0.493	4.70***	0.401	-1.15	-0.097	-1.43	-0.125
7 Sea Surface Temp.(July)	5.59***	0.369	6.97***	0.579	4.08***	0.335	-0.94	-0.076	-1.30	-0.109
8 Sea Surface Temp.(Ann.Var.)	1.69	0.114	6.23***	0.547	2.87**	0.249	-0.74	-0.064	-0.82	-0.073
9 Oxygen Minimum Layer(Depth)	4.18***	0.236	3.60***	0.191	3.75***	0.200	-0.56	-0.030	-0.79	-0.042
10 Surface Salinity	9.52***	0.594	5.31***	0.386	4.66***	0.337	0.32	0.023	-1.20	-0.088
11 Thermocline Depth(Winter)	0.40	0.026	0.90	0.070	1.88	0.144	0.20	0.016	-0.39	-0.031
12 Thermocline Depth(Summer)	1.21	0.085	-0.07	-0.007	0.84	0.079	2.60**	0.240	0.00	0.000
13 Surface Dissolved Oxygen	-1.85	-0.147	0.76	0.089	1.83	0.211	-0.40	-0.045	-0.01	-0.001
Environmental Component I	3.71***	0.238	6.75***	0.476	4.57***	0.309	-1.69	-0.111	-1.31	-0.104
Environmental Component II	3.77***	0.364	-0.26	-0.030	0.39	0.041	3.45***	0.352	2.63**	0.359
Environmental Component III	4.64***	0.449	0.52	0.059	2.36*	0.252	2.22*	0.227	4.54***	0.623

*, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

Table 8.

Comparisons of principal component and canonical variable projections for offshore *Stenella attenuata* and *S. longirostris* based on corresponding data for 16 blocks.

	Principal component		Canonical variable	
Statistic	I	II	1	2
Product-moment correlation	0.745***	0.289	0.896***	-0.328
Mantel *t*-value	3.46**	0.32	6.65***	1.62
Matrix correlation	0.528	0.039	0.741	0.204

*, $P<0.05$; **, $P<0.01$; ***, $P<0.001$. *P*-values for Mantel tests based on number of times permutational *Z*-values less than or equal to observed *Z*-values (one-tailed test).

Table 9.

Results of Mantel tests, matrix correlations, and product-moment correlations for 16 overlapping blocks of offshore *Stenella attenuata* and *S. longirostris*. Comparison of interlocality differences for 30 morphological variables.

	Character	Mantel *t*-value	Matrix correlation	Product-moment correlation
1	Condylobasal L.	1.21	0.184	0.256
2	L. Rostrum(frm.Base)	1.28	0.178	0.159
3	L. Rostrum(frm.Pterygoid)	0.55	0.074	0.150
4	W. Rostrum(at Base)	4.65***	0.626	0.837***
5	W. Rostrum(at 1/4 L.)	4.14***	0.337	0.693**
6	W. Rostrum(at 1/2 L.)	4.57***	0.495	0.775***
7	W. Premax.(at 1/2 L.)	-0.49	-0.066	0.351
8	W. Rostrum(at 3/4 L.)	1.01	0.120	0.540*
9	Preorbital W.	5.70***	0.737	0.865***
10	Postorbital W.	6.24***	0.693	0.861***
11	Skull W.(at Zygomatic P.)	6.37***	0.732	0.883***
12	Skull W.(at Parietals)	2.71**	0.446	0.616*
13	Ht. Braincase	0.60	0.093	0.294
14	L. Braincase	2.91*	0.494	0.613*
15	Max. W. Premax.	2.88**	0.318	0.675**
16	W. External Nares	-0.64	-0.073	0.224
17	L. Temporal Fossa	0.79	0.088	-0.499*
18	W. Temporal Fossa	0.62	0.077	-0.443
19	Orbital L.	0.92	0.148	0.383
20	L. Antorbital P.	4.10**	0.396	0.658**
21	W. Internal Nares	1.61	0.205	0.613*
22	L. Up. Toothrow	1.19	0.165	0.069
23	No. Teeth(Up.Lf.)	2.98**	0.501	-0.753***
24	No. Teeth(Up.Rt.)	2.99**	0.517	-0.691**
25	No. Teeth(Low.Lf.)	0.03	0.004	-0.223
26	No. Teeth(Low.Rt.)	0.66	0.104	-0.428
27	L. Low. Toothrow	0.59	0.090	0.015

Table 9. Continued.

Character	Mantel *t*-value	Matrix correlation	Product-moment correlation
28 Ht. Ramus	2.34*	0.298	0.408
29 Tooth W.	0.20	0.038	-0.260
30 L. Ramus	0.70	0.111	0.174

*, $P<0.05$; **, $P<0.01$; ***, $P<0.001$. *P*-values for Mantel tests based on number of times permutational *Z*-values less than or equal to observed *Z*-values (one-tailed test).

FIGURE CAPTIONS

Figure 1

Known range of *Stenella attenuata* in eastern tropical Pacific Ocean (based on Perrin et al. 1983), with numbers of males (above) and females (below) available for each 5° latitude-longitude block (total of 611 specimens). Each block identified by numerical code (numbers on left and bottom margins are combined; e.g., block 0802 encompasses northern Hawaiian Islands). Asterisks indicate 11 blocks included in analysis of sexual dimorphism. Initial analyses indicated specimens in four blocks (0516, 0517, 0518, 0812) represented a well differentiated inshore form (see Douglas et al. 1984); thus, these not used in subsequent evaluations. Remaining 29 blocks with two or more specimens used as basis for analyses of geographic variation; for some evaluations, eight blocks with single specimens projected onto axes based on the other 29 blocks. For 16 blocks marked with dot in lower-right corner, sufficient numbers of *S. attenuata* and *S. longirostris* (i.e., at least two of each species) available for interspecific comparison of geographic trends.

Figure 2

Correlations among characters based on character means for 29 blocks. Clustering performed using UPGMA on absolute correlations among characters (i.e., negative signs removed). Cophenetic correlation coefficient is 0.87.

Figure 3

Projections of blocks onto first two principal components based on 30 characters. Solid symbols indicate 29 blocks on which analysis conducted. Open symbols represent blocks with only single specimens projected onto axes generated from 29 blocks with two or more specimens.

Figure 4

Geographic variation in principal component I. Bar represents range (low to high block values), and midpoint is marked. Darkened part of bar indicates value for particular block.

Figure 5

Distance phenogram summarizing UPGMA clustering of 29 blocks based on 30 characters. Cophenetic correlation is 0.76.

FIGURE CAPTIONS (continued)

Figure 6

Modified skyline diagrams for 29 blocks, indicating groups formed using function-point clustering procedures and based on: (A) all 30 characters; (B) five characters that, in combination, best discriminate among blocks (Preorbital W., W. Temporal Fossa, L. Temporal Fossa, L. Rostrum[frm. Pterygoid], L. Braincase). For given *w*-value (i.e., row), blocks connected in common line are in same cluster.

Figure 7

Projections of blocks onto first two canonical variables based on 30 characters. Solid symbols indicate 25 blocks on which analysis conducted. Open symbols represent blocks with only single specimens, which were projected onto axes generated from 29 blocks with two or more specimens.

Figure 8

Geographic variation in (A) Postorbital W. and (B) canonical variable 1. Darkened part of bar indicates value for particular block.

Figure 9

Geographic variation in environmental variables as summarized in (A) principal component I and (B) principal component II. Darkened part of bar indicates value for particular block.

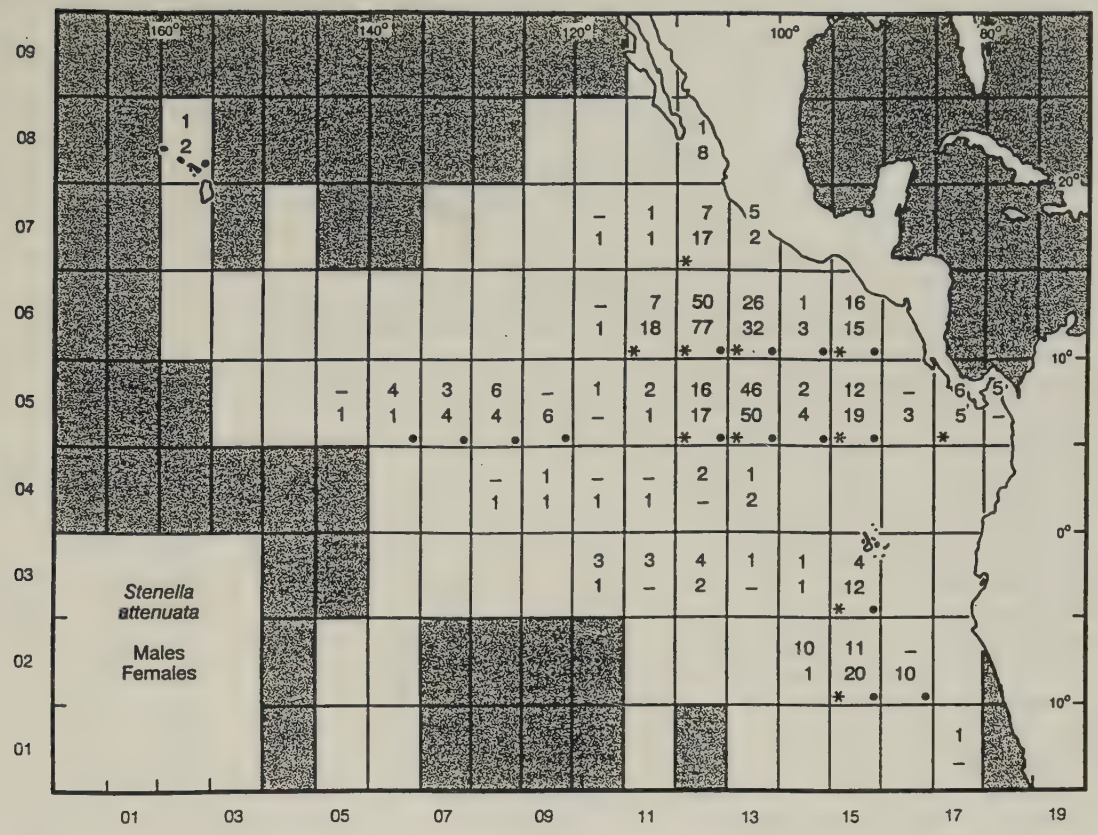
Figure 10

Geographic variation in (A) W. Temporal Fossa and (B) Sea Surface Temp.(July). Darkened part of bar indicates value for particular block.

Figure 11

Geographic variation in (A) Skull W.(at Parietals) and (B) Thermocline Depth(Winter). Darkened part of bar indicates value for particular block.

Figure 1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140°
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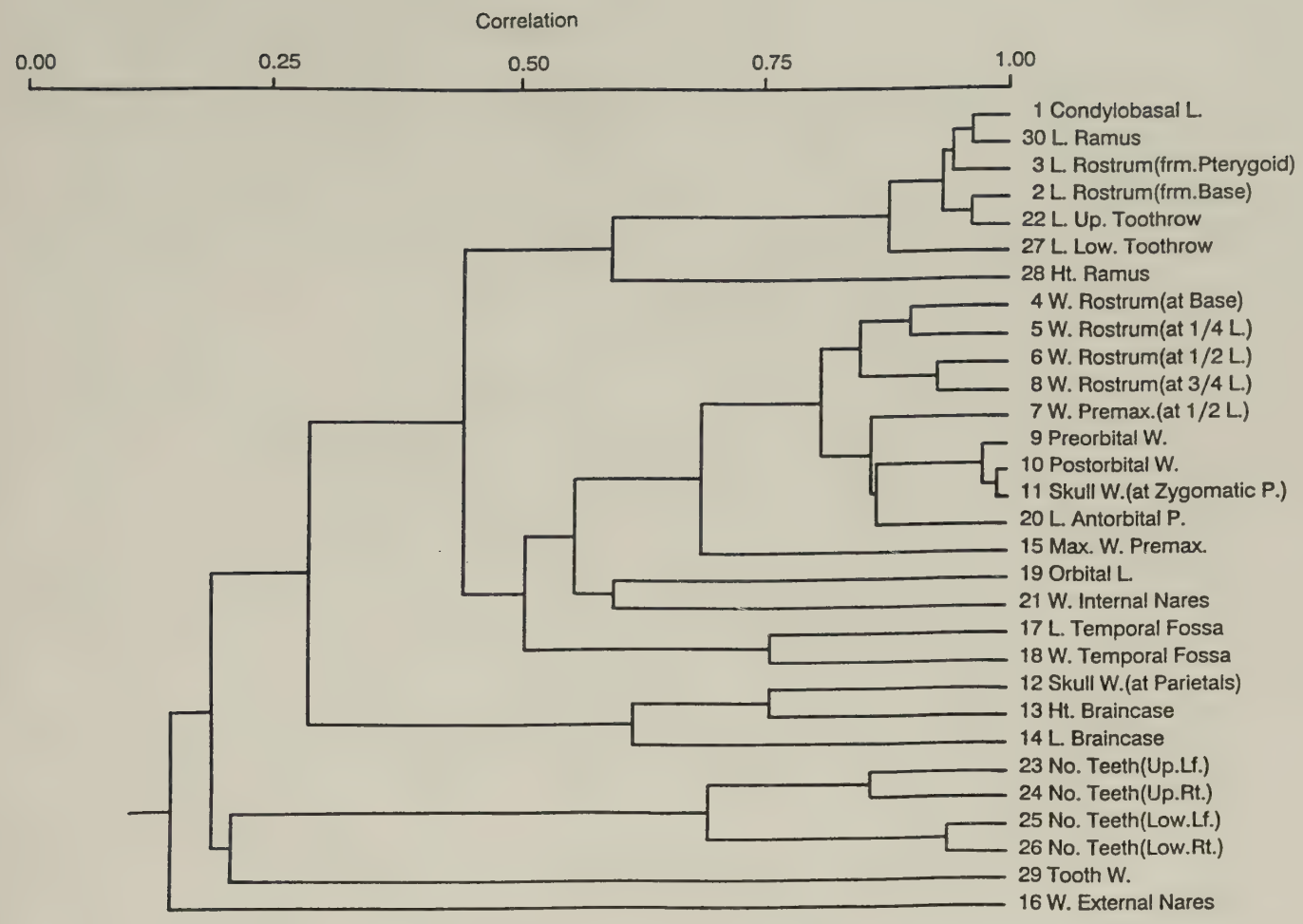
01 03 05 07 09 11 13 15 17 19
Stenella attenuata
Males
Females

Figure 2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0.50
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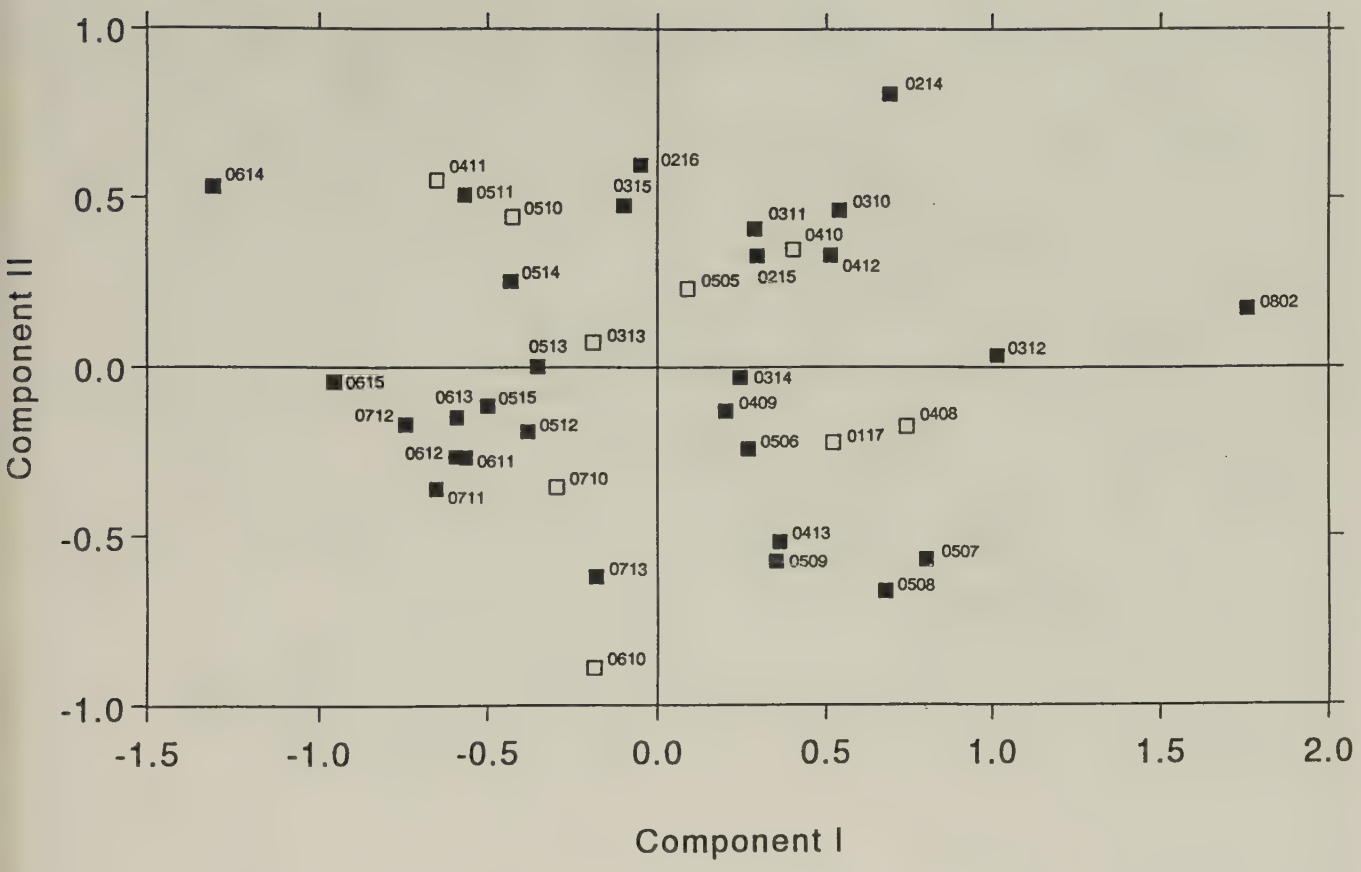
1.00
1 Condylobasal L.
30 L. Ramus
3 L. Rostrum(frm.Pterygoid)
2 L. Rostrum(frm.Base)
22 L. Up. Toothrow
27 L. Low. Toothrow
28 Ht. Ramus
4 W. Rostrum(at Base)
5 W. Rostrum(at 1/4 L.)
6 W. Rostrum(at 1/2 L.)
8 W. Rostrum(at 3/4 L.)
7 W. Premax.(at 1/2 L.)
9 Preorbital W.
10 Postorbital W.
11 Skull W.(at Zygomatic P.)
20 L. Antorbital P.
15 Max. W. Premax.
19 Orbital L.
21 W. Internal Nares
17 L. Temporal Fossa
18 W. Temporal Fossa
12 Skull W.(at Parietals)
13 Ht. Braincase
14 L. Braincase
23 No. Teeth(Up.Lf.)
24 No. Teeth(Up.Rt.)
25 No. Teeth(Low.Lf.)
26 No. Teeth(Low.Rt.)
29 Tooth W.
16 W. External Nares

Figure 3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0.0
-0.5
-1.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5
2.0
Component II
Component I
0214
0614
0411
0216
0315
0511
0510
0311
0310
0410
0514
0505
0215
0412
0802
0513
0313
0312
0615
0314
0613
0515
0409
0712
0512
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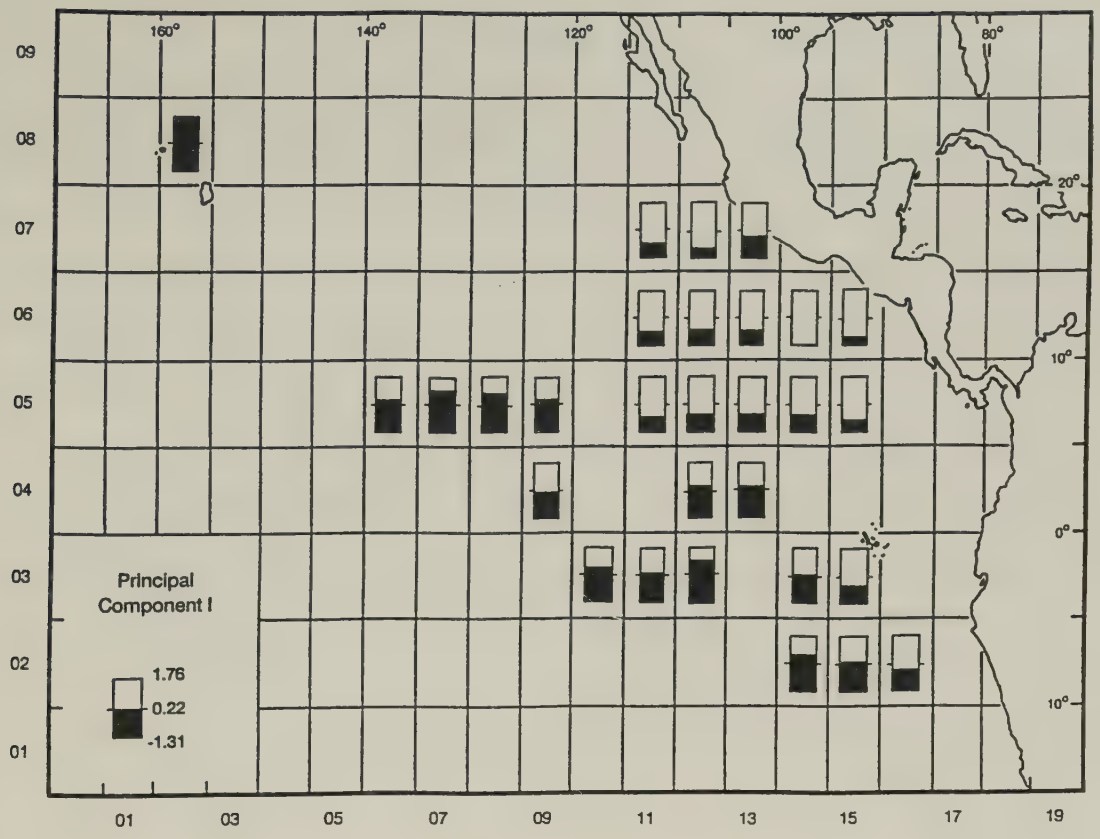
0711
0413
0509
0507
0713
0508
0610

Figure 4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09
11
13
15
17
19
Principal
Component I
1.76
0.22
-1.31

Figure 5

Distance
2.0
1.5
1.0
0.5
0.0
0214
0215
0216
0315
0412
0310
0311
0409
0413
0509
0506
0507
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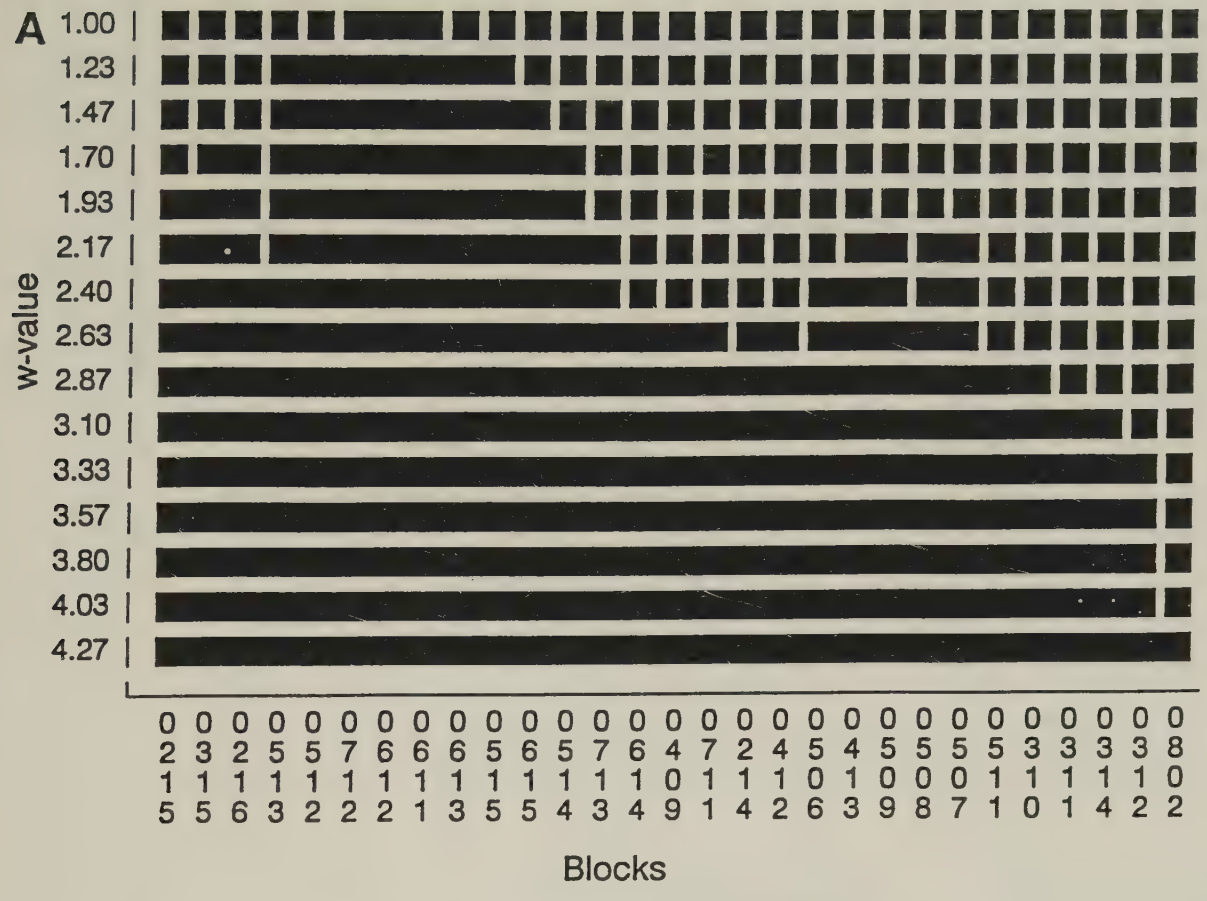
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1.93
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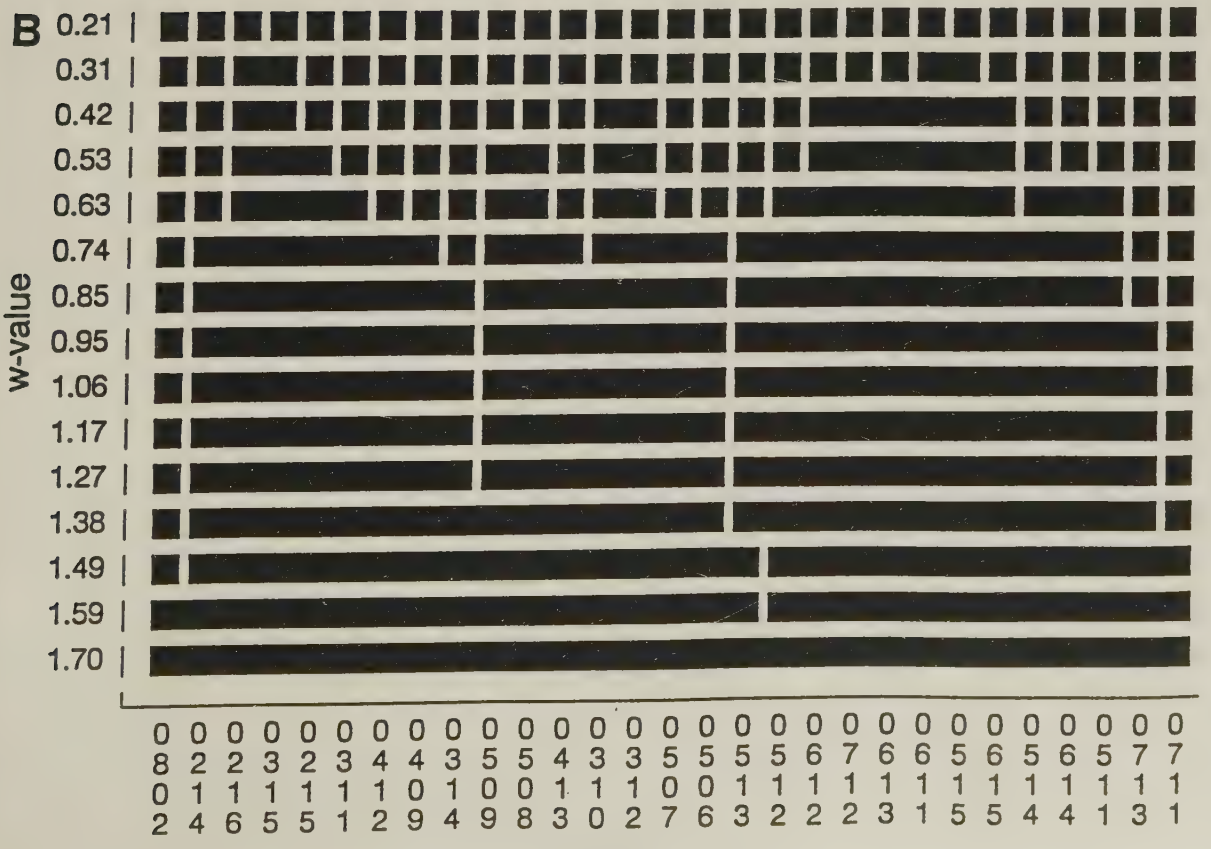
3.57
3.80
4.03
4.27
Blocks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w-value
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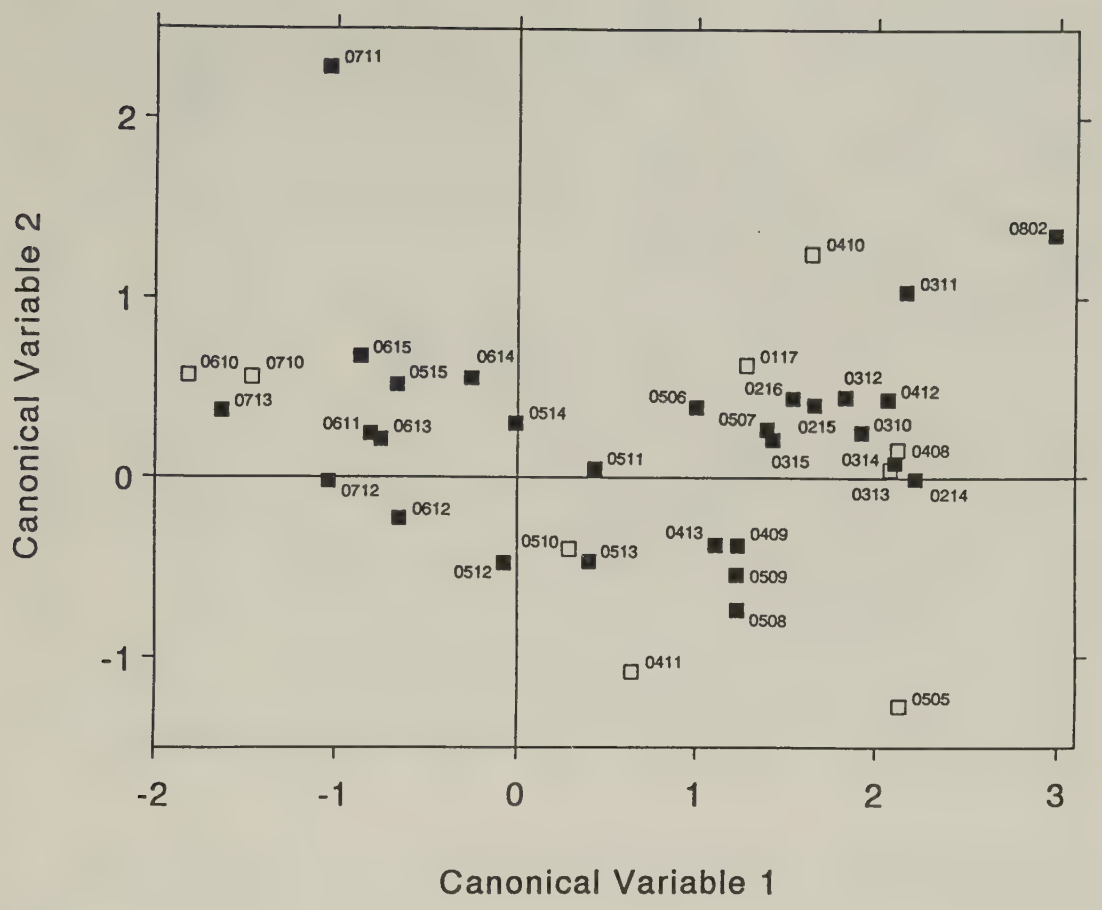
Blocks

Figure 7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0614
0515
0117
0312
0216
0412
0713
0506
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0511
0315
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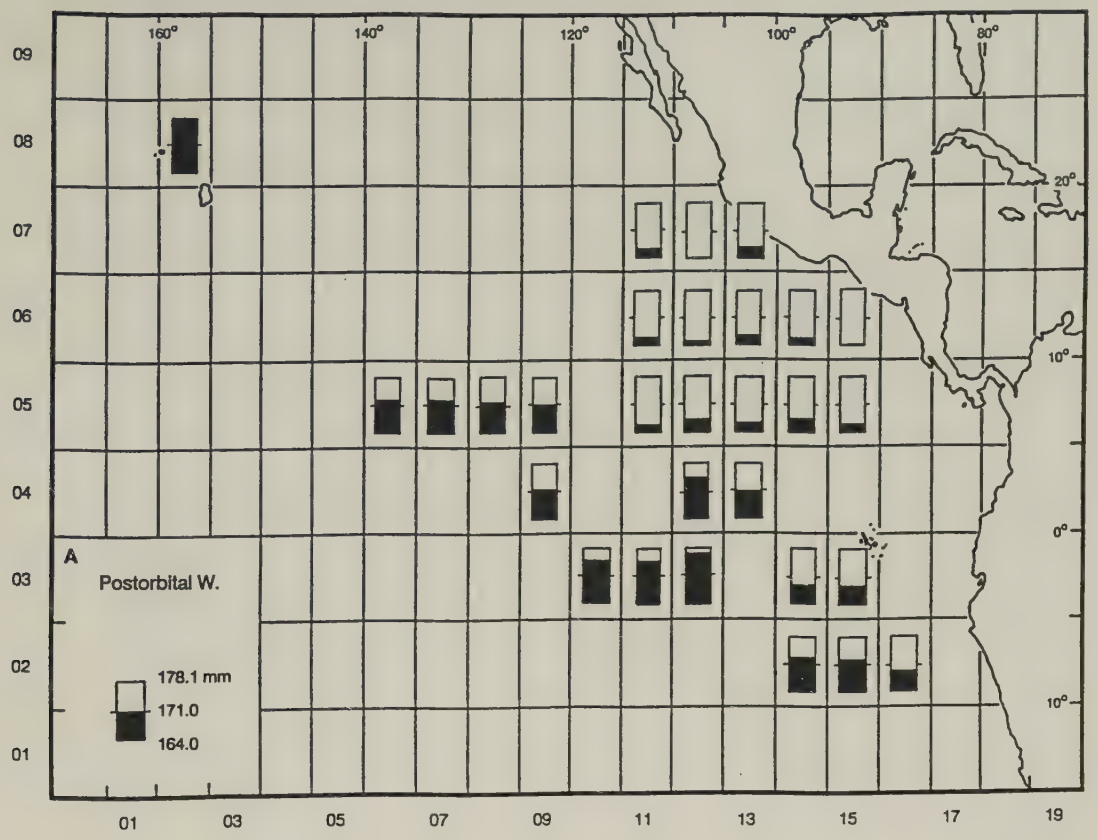
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13
15
17
19
A
Postorbital W.
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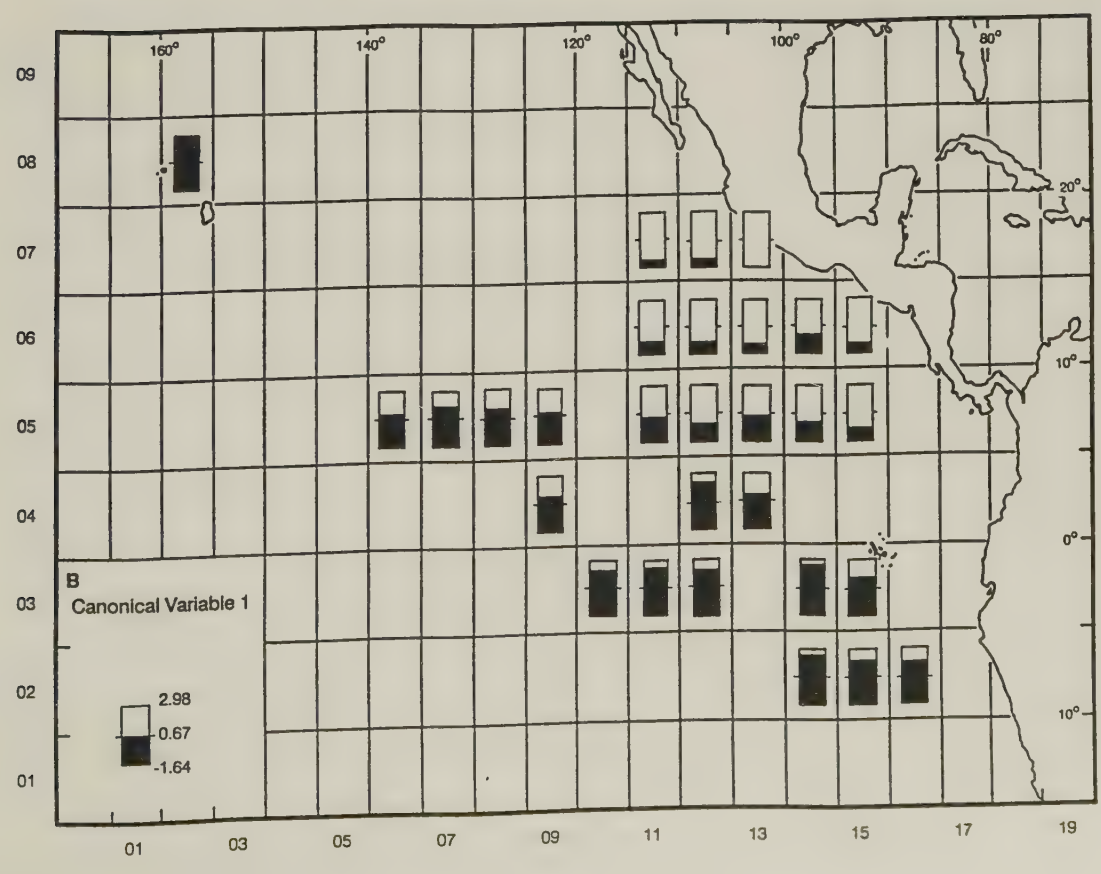
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B
Canonical Variable 1
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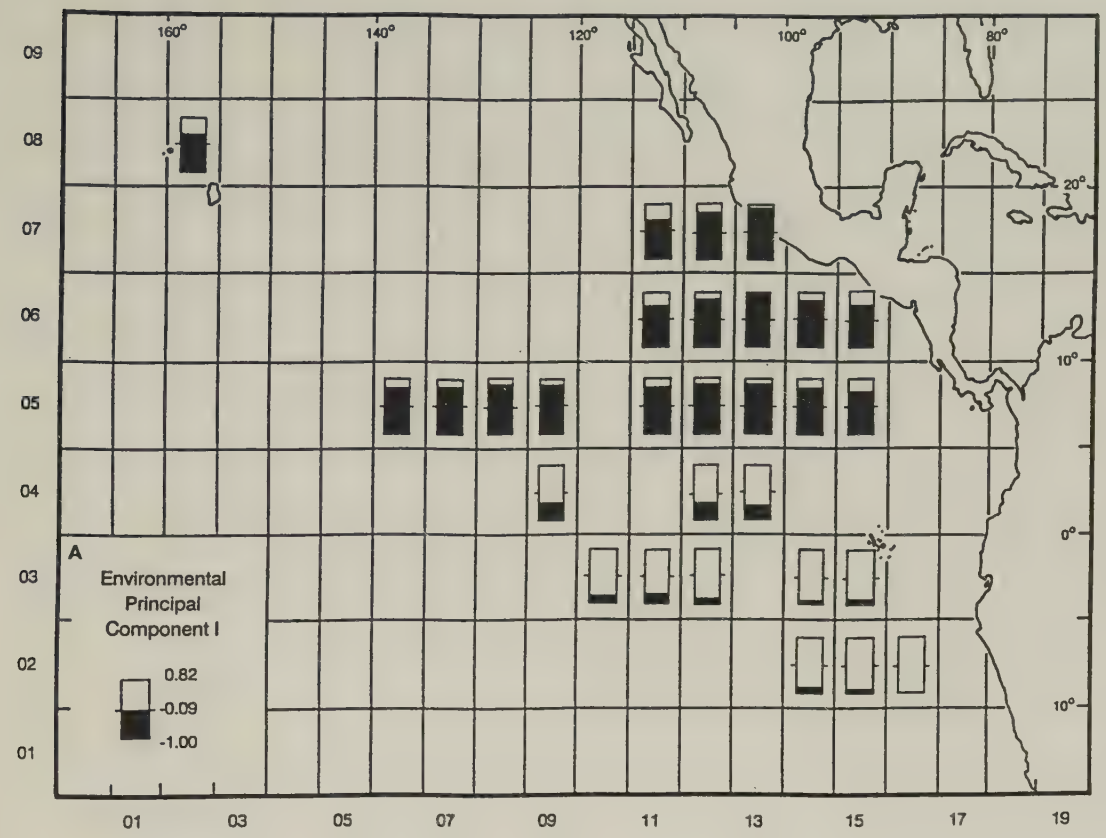
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01
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Environmental
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-1.00
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03
05
07
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11
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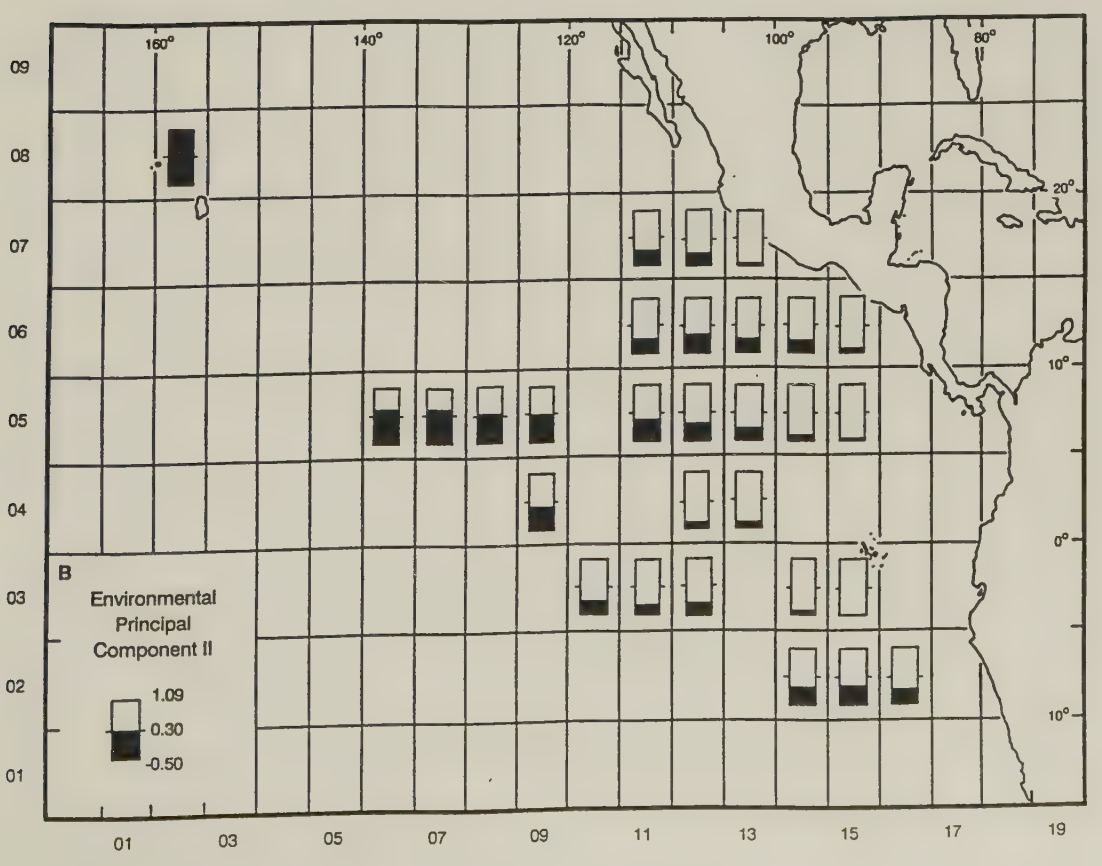
15
17
19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Environmental
Principal
Component II
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-0.50
01
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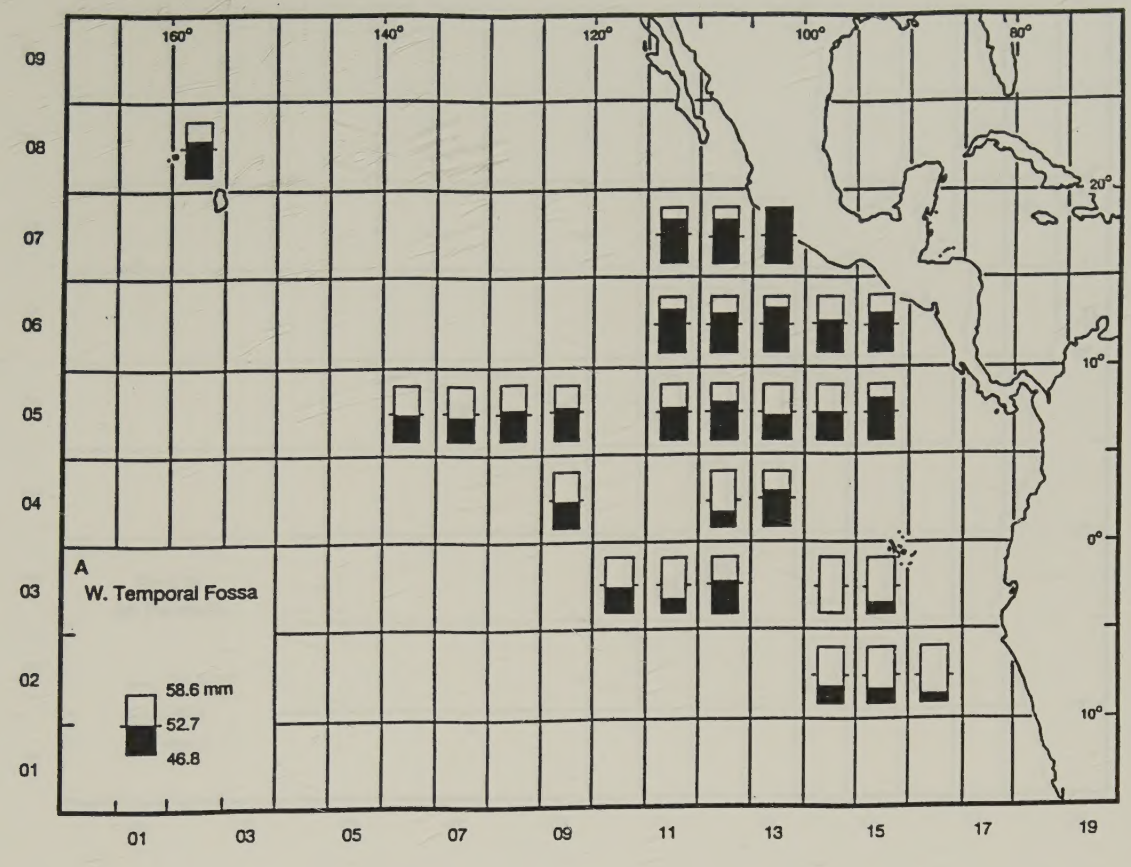
11
13
15
17
19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01
A
W. Temporal Fossa
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52.7
46.8
01
03
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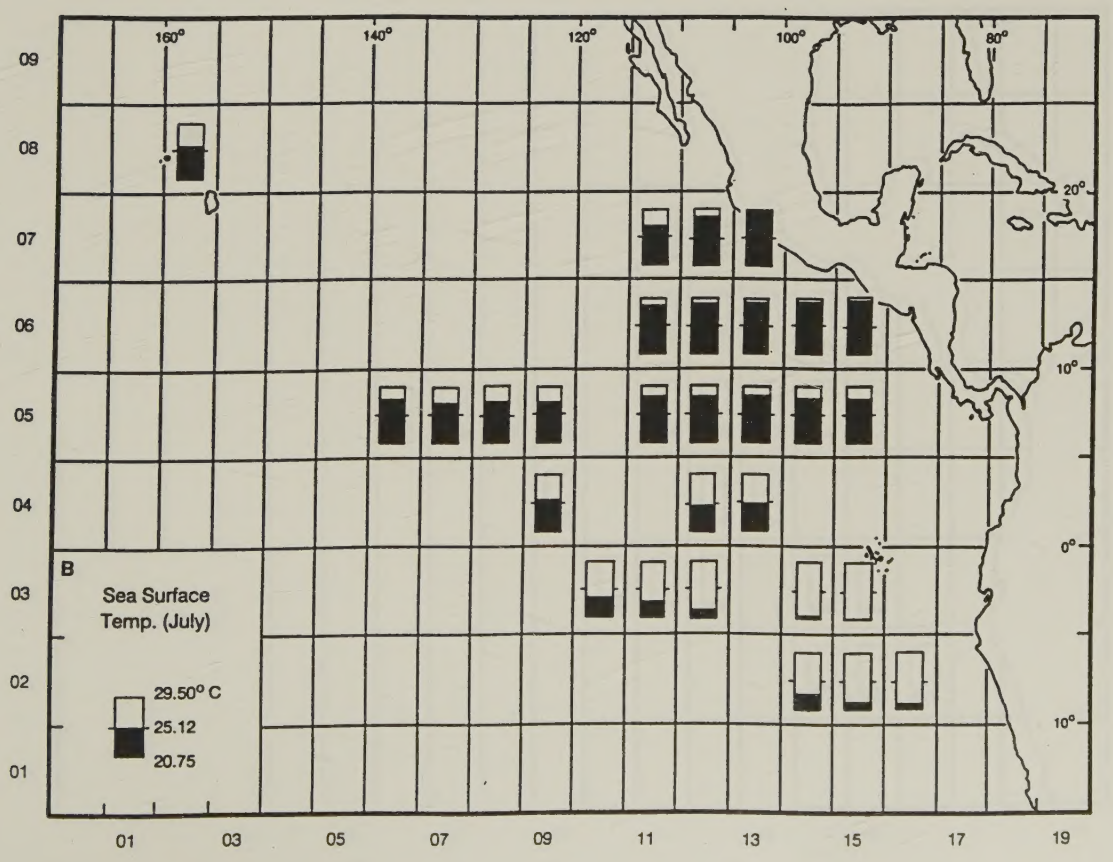
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08
07
06
05
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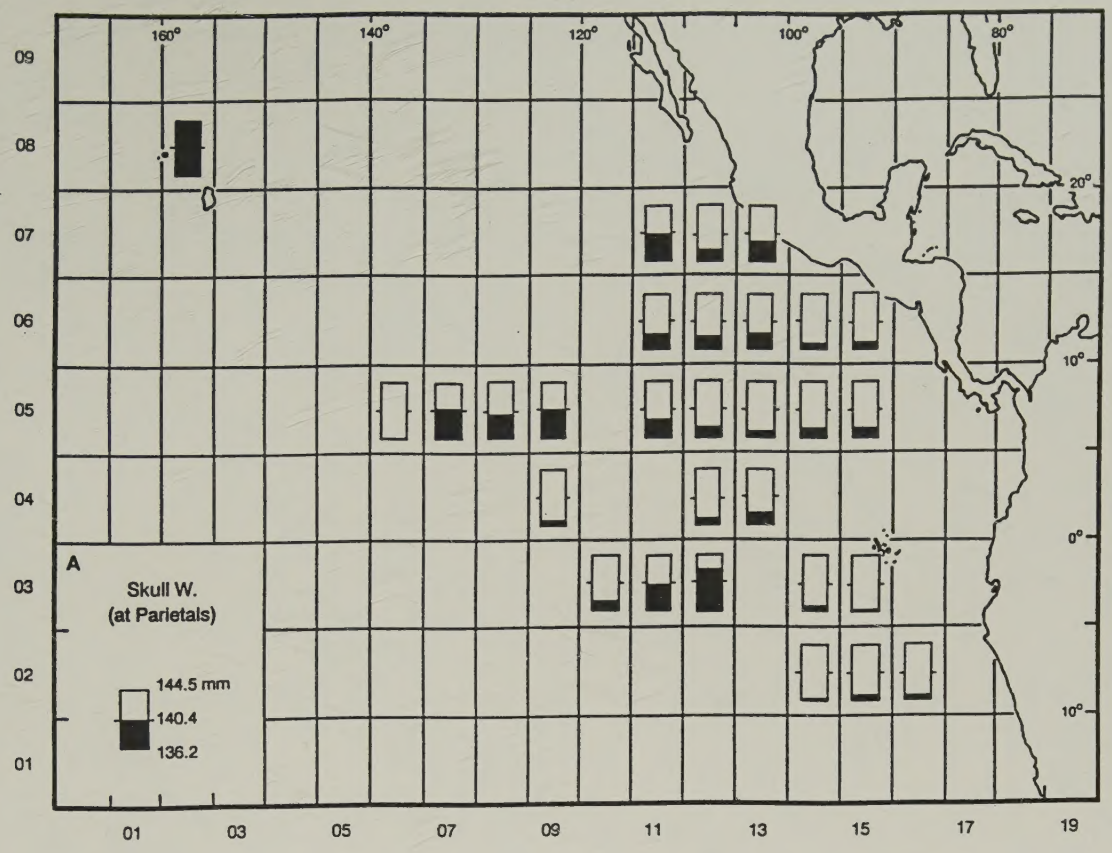
03
02
01
B
Sea Surface
Temp. (July)
29.50° C
25.12
20.75
01
03
05
07
09
11
13
15
17
19

Figure 11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13
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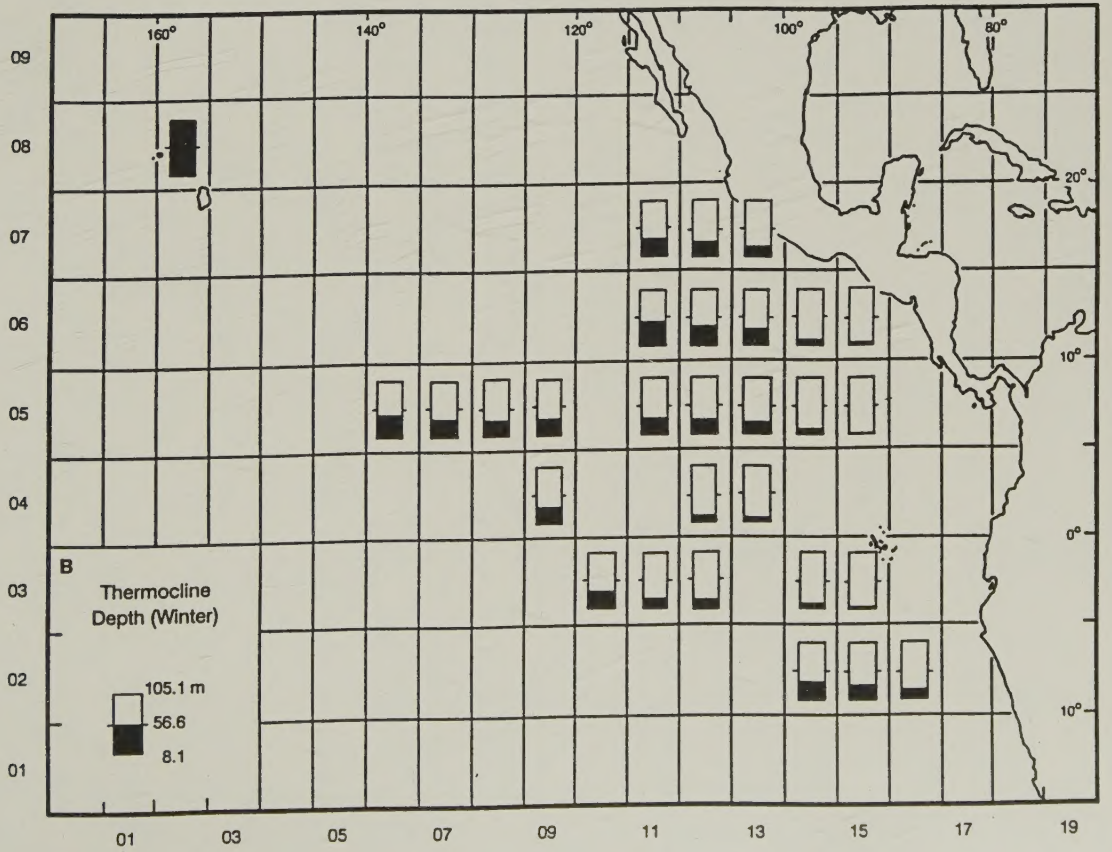
17
19
A
Skull W.
(at Parietals)
144.5 mm
140.4
136.2


160°
140°
120°
100°
80°
20°
10°
0°
10°
09
08
07
06
05
04
03
02
01
01
03
05
07
09
11
13
15
17
19
B
Thermocline
Depth (Winter)
105.1 m
56.6
8.1